Letters to the Editor

Stratification and disconformities in yellow sands of the Bassendean and Spearwood Dunes, Swan Coastal Plain, South-western Australia: discussion.

A recent article in the Journal of the Royal Society of Western Australia (Glassford & Semeniuk 1990) provided evidence for arid phase transport of Bassendean and Spearwood Dunes of the Swan Coastal Plain. While agreeing with many of the conclusions, I note on page 77 a report of no previous work on stratification of the deposits, on page 78 that the age is mainly mid-Pleistocene, and on page 88 that wind directions were mainly from the east. Various 'overprint' features are listed on page 90 without any mention of human activities, yet the latter are well known on the Plain, sometimes from deposits one or two metres deep with Holocene carbon dates (for example, Pearce 1981).

Some of these locations indicate deflation, but others certainly show accumulation of aeolian sediments, and the question remains, were they localised and related to disturbance of occupation, or were they part of a wider mobility of upper layers of soil during the Holocene?

Further, although Walyunga is not on the coastal plain it does contain a large dune 5.1 m deep formed by easterly winds, where the upper 1.9 m contains stratified sandy soil with occupation debris spanning most of the Holocene (Pearce 1978). It even shows good evidence of a mid-Holocene hiatus possibility linked to aridity.

Finally the Upper Swan site has alluvial deposits but it is close to Bassendean dunes and its dated soil profiles provide some clues to late Pleistocene changes (Pearce 1983).

Such studies and others published (Hallam 1987) and unpublished show that there was intermittent human usage of parts of the Swan Coastal Plain, and such studies should contribute towards interpretation and understanding of its development.

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References

Hallam S J 1987 Coastal does not mean littoral. Australian Archaeology 25:10-29.

Glassford D K & Semeniuk V 1990 Stratification and disconformities in yellow sands of the Bassendean and Spearwood Dunes, Swan Coastal Plain, South-western Australia. Journal of the Royal Society of Western Australia 72:75-93.

Pearce R H 1978 Changes in artifact assemblages during the last 8,000 years at Walyunga, Western Australia. Journal of the Royal Society of Western Australia 61:1-10.

Pearce R H 1981 Artifact usage and sea level changes. The Artifact 6:30-33.

Pearce R H 1983 Archaeology by system and chance. In: Archaeology at ANZAAS 1983 (ed M Smith) Western Australian Museum, Perth, 350-358.

Stratification and disconformities in yellow sands of the Bassendean and Spearwood Dunes, Swan Coastal Plain, South-western Australia: reply.

We welcome the opportunity provided by Pearce's letter to discuss aspects of our recent paper (Glassford & Semeniuk 1990).

In relation to our statement that generally there has been no previous work on stratification in yellow sands, we emphasise that our comments concern primary sedimentary statification in the yellow sands, and not the gross layering which locally is evident. The gross layering is due to either secondary alteration (pedogenic/diagenetic), or the superimposition of successive units which exhibit these secondary alteration features.

Human activities are suggested by Pearce as an agent for alteration of yellow sand. While we accept in principle that anthropogenic activities can alter and perturbate yellow sand in the younger parts of the sequence, we did not unequivocally detect the products of any such activity at our study sites. Our study concentrated on the description of primary stratification features in deep sequences of the yellow sands, as a basis for interpreting the primary sedimentary origin of such sequences. We described the types of alteration in these sands only as a basis for interpreting overprint features, to enable us to peer through the alteration effects. In our study the alteration features were overwhelmingly biological such as humification, or bioturbation by vegetation and fauna (e.g., termitarium structures), and chemical, such as bleaching and cementation. In regards to anthropogenic alteration effects, we also envisage that it would be more probable to detect such effects in areas where human occupation may have been more likely, that is, near river courses such as at Walyunga, or near estuaries such as at Mosman, where to date they have been mostly found. Our study sites, however, were well away from such localities. It is apparent that the bulk of the yellow sand pre-dates 10,000 years, and even c. 50,000 years, the approximate time that humans are believed to have arrived in Australia, so we do not expect that there should be evidence of human alteration in the deeper sequences of the yellow sand. These deeper sequences form the major bulk of the yellow sands.

Now for the matter of the the age of the yellow sand sequences. We have no problem in accepting Holocene ages that have been obtained from radiocarbon dating of charcoal from the upper parts of the yellow sand sequences. However, such dates must be viewed as chronicling events only in the upper, near-surface parts of the yellow sand sequences. This surficial zone is also the only place in the yellow sand sequences where the radiocarbon material is located. These radiocarbon dates therefore should not be construed or extended to infer ages for the entire sequence of the yellow sand throughout all parts of the Swan Coastal Plain. For instance, it it is possible that the sand overlying the uppermost disconformity at Site 7 (Fig. 3) was emplaced in the Holocene. But such a date should not be extrapolated throughout the whole sequence as the age of all the underlying sands and disconformities. Evidence of other authors also shows that yellow sand *underlies* Tamala Limestone. Thus, these yellow sands

predate the limestone, and hence must be at least Pleistocene. A Holocene age for the upper, surficial part of a thick yellow sand sequence, or a Holocene age for an isolated outlier of yellow sand, should not be used to derive an age for the entire yellow sand sequence elsewhere. We envisage that the upper, surficial part of the yellow sands had phases of activity and mobility during the early to mid Holocene, and during these times, human occupation sites in this region could be expected to be buried. At present we are preparing a paper (Semeniuk & Glassford, in prep.) on the remobilisation of yellow sands in coastal areas. This will explain some of the ages and sequences evident in yellow sands near the coast.

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Reference

Glassford D K & Semeniuk V 1990 Stratification and disconformities in yellow sands of the Bassendean and Spearwood Dunes, Swan Coastal Plain, South-western Australia. Journal of the Royal Society of Western Australia 72:75-93.

Recent Advances in Science in Western Australia

Earth Sciences

Much of the Fortescue Group in the Hamersley Basin is older (2765-2687 Ma) than the Yilgarn granite-greenstone terrane according to N T Arndt of the Max-Planck-Institut für Chemie, Germany, and Australian colleagues. The platform cover was being deposited on the Pilbara granite-greenstone terrane while the Yilgarn granite-greenstone terrane was still being developed:

Arndt N T, Nelson D R, Compston W, Trendall A F, & Thorne A M 1991 The age of the Fortescue Group, Hamersley Basin, Western Australia, from ion microprobe zircon U-Pb results. Australian Journal of Earth Sciences 38:261-281.

A useful synthesis and interpretation of seafloor spreading around Australia from 160 Ma to present, based on changes in plate geometry, is provided by J J Veevers and colleagues of the Macquarie University School of Earth Sciences:

Veevers J J, Powell C McA & Roots S R 1991 Review of seafloor spreading around Australia. 1. Synthesis of the patterns of spreading. Australian Journal of Earth Sciences 38:373-389.

Precambrian geological history of the Hamersley basin is interpreted in terms of plate tectonics by I M Tyler of the Geological Survey of WA. After development of the Fortescue and Hamersley Groups (2750-2300 Ma), a convergent phase began as a result of a collision between the Pilbara and Yilgarn Cratons resulting in the Capricorn Orogeny (2200-1600 Ma):

Tyler I M 1991 The geology of the Sylvania Inlier and the southeast Hamersley Basin. Western Australia Geological Survey, Bulletin 138.

Detailed biostratigraphy has been used by J Backhouse of the Geological Survey of WA to correlate the coal seams in the Collie Basin and to compare them with the Karoo Basin in South Africa, demonstrating the value of pollen analysis in predicting the age of coal seams:

Backhouse J 1991 Permian palynostratigraphy of the Collie Basin, Western Australia. Review of Palaeobotany and Palynology 67:237-314.

Two stages are recognised in the evolution of the southern transform margin of the Exmouth Plateau - rifting and shearing, followed by drifting with igneous intrusion and underplating - according to J M Lorenzo of the Lamont-Doherty Geological Observatory, New York, and colleagues at the Bureau of Mineral Resources, Canberra:

Lorenzo J M, Mutter J C, Larson R L *et al.* 1991 Development of the continent-ocean transform boundary of the southern Exmouth Plateau. Geology 19:843-846.

Life Sciences

Banksia cuneata is the rarest of the 76 *Banksia* species, with only 350 plants surviving. The most limiting factor in regeneration after fire-induced seed release was survival over the first summer (less than 0.1% of seedlings in this study by Lamont and colleagues of the Curtin University of Technology), and survival was greatly improved by regular watering or transplanting to moister sites:

Lamont B B, Connell S W & Bergl S M 1991 Seed bank and population dynamics of Banksia cuneata: the role of time, fire, and moisture. Botanical Gazette 153:114-122.

The term serotiny is suggested by B B Lamont at Curtin University of Technology as the most appropriate term for plants that retain some of their seeds for more than a year - this phenomenon is more widespread among shrubs and trees of south-western Australia than anywhere else in the world:

Lamont B B 1991 Canopy seed storage and release - what's in a name? Oikos 60:266-268.

Lupin yields were improved by 10-90% when superphosphate was banded 5-8 cm below the seed compared with banding with the seed, and was decreased by 30-60% by topdressing P, according to R J Jarvis and M D A Bolland of the WA Department of Agriculture. Banding improved root interception and uptake of P:

Jarvis R J & Bolland M D A 1991 Lupin grain yields and fertiliser effectiveness are increased by banding superphosphate below the seed. Australian Journal of Experimental Agriculture 31:357-366.

Note from the Hon Editor: Members and non-members of the Royal Society of Western Australia are encouraged to submit Letters to the Editor and contributions to Recent Advances in Science in Western Australia. For the latter, please provide short (2-3 sentence) summaries of recent significant papers by Western Australian scientists or others writing about Western Australia, together with a copy of the title, abstract and authors' names and addresses, to the Hon Editor or a member of the Publications Committee: Dr S D Hopper (Life Sciences), Dr A E Cockbain (Earth Sciences), and Assoc Prof J Webb (Physical Sciences). Final choice of articles is at the discretion of the Hon Editor.

Comparison of three methods of forecasting 24-hour tropical cyclone movement in the Western Australian region

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Abstract

Three methods of forecasting tropical cyclone tracks in the Western Australia region are discussed. One is a version of Neumann's CLIPER adapted for the region and referred to as CPLR, another is a method developed in Western Australia which uses the low-level relative vorticity field in the environment of the cyclone as a predictor, and the last is pure persistence. The three methods were used to produce 214 triplets of forecasts from best-track data for 13 cyclones and the results compared. The Wilcoxon test was used to test the significance of differences between forecasts for various subsets of cyclones. The results suggest that (a) the performances of the first two methods match that of persistence overall, and are superior when the error in the persistence forecast is greater than the mean error or when the cyclones are recurving, and (b) the second method matches CPLR overall and surpasses it with some categories of cyclones.

Introduction

The 'Tropical Cyclone Study Group' based at Murdoch University, Western Australia, for some years worked on methods of improving the forecasting of cyclone tracks in the northwest of the State. Most effort was expended on two methods that do not require upper-level wind data, which are lacking in the region; namely, a version of Neumann's (1972) CLIPER developed by Lyons and Joyce (1983) and named CPLR, and a method due to Hopwood (1978). This latter method (known as the vorticity method) uses an estimate of the vorticity in the low-level environment of the cyclone in combination with the current velocity as a predictor of the cyclone movement. CPLR uses a combination of persistence and climatology and so produces its largest errors when applied to cyclones with rapidly varying or unusual tracks. It is generally thought that cyclone motion is determined by the surrounding flow integrated in some fashion through the depth of the troposphere, but in practice it is common to take a few or even one level as representative of the whole flow, on the grounds that different levels in the atmosphere are coupled through vertical motions, which though small (except in special regions such as cumulo-nimbus cells) are not identically zero. For example, George and Gray (1976) found that the 500 mb wind averaged over an annular region between one and seven latitude degrees from the cyclone centre was the best predictor of the direction of cyclone movement while the 700 mb wind averaged in the same way was the best predictor of speed. The method CPLR cannot use explicitly any wind or pressure data at all but the persistence component incorporates it implicitly. The vorticity method also does this and in addition uses observations of surface pressure, which one would expect to reflect to some degree conditions in the overlying atmosphere.

Each method was used to produce 214 forecasts for 13 cyclones which occured in the Western Australian region during the 1979-80 and 1980-81 seasons and the resulting errors were compared with the corresponding errors produced by (a) the other method, and (b) a pure persistence forecast using average velocity over the preceding six hours as current velocity. All 642 forecasts were produced by computer routines developed by members of the Study Group. This facilitated the making of a large number of forecasts without the subjectivity of hand forecasts but, as explained later in the paper, disadvantaged the vorticity method.

CPLR

Lyons and Joyce (1983) used all available storm-track data from the Australian Bureau of Meteorology archives for storms off the north-west coast of Australia for the period 1906-1980. These data were used to produce a regression analysis (known as CLIP) with simple as well as cross terms of degrees one, two, and three following Neumann (1972). Stepwise screening regression was used to select the best combinations of predictors from the set of all possible combinations. Runs were ended when an additional predictor failed to lower the variance by at least 0.5 percent. A greater number of storm days was available than for either the Atlantic or Eastern Pacific versions of CLIPER though there were fewer storms. Also, two least-squares fits were done, one using a first-order and the other

Table 1

Twentyfour-hour errors in forecast position (nautical miles)

	CLIP	CPLR	Number of forecasts
Felix	100	95	8
Mable	97	86	8
Neil	87	81	10
Max	97	75	7

Table 2
Eight primary predictors for CPLR (after Lyons and Joyce (1983))

Predictor	Physical value	Comments
P_1	latitude at time t	
P_2	longitude at time t	
P_3	v component of storm velocity at time t	from positions @ t & t–12
P_4	u component of storm velocity at time t	from positions @ t & t–12
P_5	v component of storm velocity at time t–12	from positions @ t–12 & t–24
P_6	u component of storm velocity at time t–12 hours	from positions @ t–12 & t–24
P_7	central sea level pressure	pressure in millibars
P_8	day number	day 1 = 1 July; day 185 = 1 Jan

a second-order polynomial of the eight primary predictors (listed in Table 2). Surprisingly, the simpler linear fit proved to be more statistically significant than the second-order version and comparable in significance with CLIP. This is illustrated by a comparison, presented in Table 1, of CLIP results with results of the simpler version (here called CPLR for Climatology Persistence Linear regression) for four cyclones.

Vorticity method (AVM)

This method is based on the observation that cyclone tracks in the west Australian region appear to be affected by interaction between the cyclonic circulation and the low-level environmental flow. It requires the identification of the position of maximum value of the quantity $\xi = k.\nabla \times (k\nabla \times p)/(f\rho)$ in the 900 m flow within a 12 latitude degree radius of the cyclone; i.e. of the position where the cyclonic relative vorticity would be greatest were the flow geostrophic. Here p denotes pressure, f the Coriolis parameter, ρ density and k a unit vector in the vertical direction.

The original justification for the method was entirely empirical. A frequent feature of summertime synoptic situations in Western Australia is a trough at or near the coast, and it was known that cyclones often, but not always, move into the trough. Perusal of the records led to the conclusion that a property common to almost all instances (of those studied) of cyclones moving into the trough and absent from almost all others was cyclonic vorticity in the trough. Further investigation (Hopwood 1978) suggested that cyclones are attracted by cyclonic vorticity maxima, whether associated with a trough or not. Attempts have been made to produce a theoretical explanation of the effect, and an account of a mathematical model of a proposed mechanism is currently being prepared for publication. We give a brief summary of it here. First, a strong vorticity maximum corresponds to a region where wind and pressure fields are not in balance. The process of adjustment produces low-frequency inertial/gravity waves radiating outwards. Secondly, the very small-amplitude geopotential disturbance this produces interacts with the high Rossby-number flow in the eye-wall region of a cyclone in such a way as to cause subsidence on one side of the eyewall and upward motion on the other, thereby producing a deepening of the eye in the region of greatest upward movement and a filling on the opposite side. This produces an effective 'movement' or propagation of the storm in the direction of the enhanced upward motion.

The forecasts were made objectively using an automated computer-based scheme with the following rules:

(i) Apply a deceleration of magnitude 0.1 lat. deg./(6 hours)^2 and maintaining the initial bearing for 12 hours or until the cyclone is stationary, whichever is sooner, then

(ii) apply an acceleration of magnitude 0.1 deg.lat./(6 hours)^2 towards the vorticity maximum for the remainder of the forecast period.

(iii) If there is no vorticity maximum maintain initial velocity.

These rules follow the scheme described in Hopwood (1978) except that the forecast is based on acceleration rather than velocity. They incorporate a measure of persistence but no climatology. Observations of the behaviour of west Australian cyclones between 1978 and 1986 and the theoretical work referred to above suggest that the magnitude of the acceleration ought to depend on the strength of the vorticity maximum and the strength of the cyclone. However, for practical reasons and to maintain an objective forecast the forecasts were all made automatically using the same magnitude of acceleration. The given value of the acceleration was chosen because in a preliminary analysis of a sample of six cyclones it gave the best mean result. These cyclones were not included in the set used for the comparison with CPLR.

Calculation of vorticities from standard meteorological data is difficult because it involves estimating second-order differences in a pressure field. An automated scheme developed by Scott *et al.* (1982) uses optimal triangular nets to produce a 'best set' of vorticities from a set of pressure and temperature data (Magnus *et al.* 1983). Quite good forecasts were produced but unfortunately the procedure proved too time-consuming for operational use. Therefore the scheme was abandoned and instead Surface II (Sampson 1975) was used to produce contours of 900 m pressure and temperature on a 2.5 degree grid. Surface II is an algorithm which interpolates to produce data on a square pattern in a Cartesian framework of latitude and longitude. Finite differences are then used to estimate the vorticity at each grid-point. One effect of this latter approach is to smooth out the vorticity field considerably. A comparison of some of the results with corresponding hand-drawn 900 m charts suggests that on some occasions the smoothing even causes the position of the vorticity maximum to be wrongly identified, assuming that the position on the hand-drawn chart is correct. The Automated Vorticity Method (hereinafter known as AVM) thus enters the comparison contest considerably handicapped.

Comparison of methods

The three forecasting schemes were used to produce 214 24-hour forecasts for 13 cyclones using synoptic data for 0500 GMT, 1100 GMT, 1700 GMT and 2300 GMT. A list of the cyclones is given in Table 3. Each forecast position was compared with the corresponding best-track position, and forecast position and direction errors produced for each

Table 3
Cyclones used in the comparison

Cyclone	Period		
Amy	6 — 11	January	1980
Brian	20 — 27	January	1980
Clara	22 — 27	January	1980
Dean	30	January	1980
Enid	14 — 16	February	1980
Gloria	21 — 27	March	1980
Carol	13 — 23	December	1980
Dan	16	December	1980
Felix	23 — 29	December	1980
Edna	21 — 25	December	1980
Mabel	13 — 19	January	1981
Neil	26 — 5	Feb/Mar	1981
Max	14 — 17	March	1981

scheme. The non-parametric Wilcoxon test was applied to various subsets of errors in order to test the significance of the differences between the errors. This test, which takes account of the magnitude as well as the sign of the differences, requires that the data be serially independent. Independence was tested for by using the run test on the set of error differences for each cyclone. A run is a set of successive differences of the same sign and either an abnormally high or an abnormally low number of runs indicates lack of independence. The results of the test led us to accept the hypothesis that the data are independent. This is not to say, of course, that the positions of a cyclone at two times six hours apart are not correlated, but rather that the success of one forecasting method relative to another at one time is independent of its success at a time six hours before or after.

Tables 4 to 8 show the results of the comparison of errors: table 4, all cyclones in the sample; Table 5, all cyclones at latitudes poleward of 20°S and all cyclones equatorward of 20°S at forecast time: Table 6, all cyclones which were moving eastward and all cyclones which were moving westward at forecast time: Table 7, all cyclones for which the error in the persistence forecast was greater than the mean (101 nautical miles), and Table 8, all recurving cyclones. This last category consisted of the four cyclones which changed from westward movement at forecast time to eastward movement at some time during the following 24 hours. Only the first such forecast for each cyclone was counted because subsequent forecasts were not independent and so the sample was too small to justify application of a statistical test.

Each table shows the mean position error (that is, the mean distance between forecast and actual position), the mean error in forecast direction, latitude and longitude, the standard deviations of the position errors, and P, which is the probability of obtaining a Wilcoxon test statistic less than the one actually obtained, under the null hypothesis that both sets of errors come from populations with the same mean. Square brackets indicate that only the magnitude of the quantity is considered. Differences were calculated by subtracting the error of the method with the smaller mean error from the corresponding error of the method with the larger mean error. The test statistic was the sum of the negative ranks; that is, a small value of P indicates that the method with the smaller mean error is probably superior. A positive direction error means that the forecast position lay to the right of the actual track; a positive latitude (longitude) error means that the forecast position was too far to the south (east). Units are nautical miles and degrees.

Table 4
All cyclones, 214 forecasts.

Mean Error in	CPRL	AVM	Persistence
Position	101.5	104.5	101.3
[Direction]	23.9	26.0	23.9
[Latitude]	1.0	1.1	1.1
[Longitude]	1.2	1.2	1.1
Direction	− 2.2	3.7	3.0
Latitude	0.1	− 0.3	− 0.1
Longitude	0.2	0.2	− 0.2
S.D. Dist	69.9	66.6	70.2

P	Position	|Direction|
AVM vs CPLR	.09	.10
CPLR vs Persistence	.50	.74
AVM vs Persistence	.05	.07

Table 5
The effect of latitude

Mean error in	Cyclones poleward of 20°S 32 forecasts			Cyclones equatorward of 20°S 182 forecasts		
	CPLR	AVM	PER	CPLR	AVM	PER
position	158.5	132.7	138.3	91.4	99.5	94.8
[Direction]	− 32.3	27.3	28.0	22.4	25.7	23.2
[Latitude]	1.6	1.6	1.6	0.9	1.0	1.0
[Longitude]	2.0	1.5	1.5	1.1	1.1	1.1
Direction	− 6.0	11.1	13.1	− 1.5	2.4	1.2
Latitude	0.1	0.0	0.5	0.1	− 0.4	− 0.2
Longitude	0.8	− 0.9	− 1.1	0.0	0.5	0.0
S.D. Dist	76.1	61.2	67.4	63.6	66.3	68.7

P	Position	|Direction|	Position	|Direction|
AVM vs CPLR	.05	.05	.01	.01
CPLR vs Persistence	.09	.09	.17	.14
AVM vs Persistence	.15	.12	.01	.02

Table 6
The effect of east-west movement

Mean Error in	Cyclones moving east 51 forecasts			Cyclones moving west 162 forecasts		
	CPLR	AVM	PER	CPLR	AVM	PER
Position	139.3	130.0	132.8	89.3	96.3	91.2
[Direction]	35.8	29.9	34.6	19.3	23.0	20.5
[Latitude]	1.5	1.6	1.4	0.9	1.0	1.0
[Longitude]	1.7	1.4	1.5	1.0	1.1	1.0
Direction	19.5	9.5	− 2.2	− 5.7	6.4	4.6
Latitude	− 0.1	− 0.5	− 0.1	0.1	− 0.3	0.0
Longitude	− 0.8	− 1.1	0.1	0.3	0.4	− 0.3
S.D. Dist	83.6	83.5	95.7	59.9	52.8	56.2

P	Position	|Direction|	Position	|Direction|
AVM vs CPLR	.04	.04	.006	.005
CPLR vs Persistence	.13	.13	.20	.04
AVM vs Persistence	.21	.04	.01	0

Table 7
The effect of 'difficulty'

Cyclones for which persistence error greater than 101 nmi   93 forecasts

Mean error in	CPLR	AVM	Persistence
position	149.4	155.3	160.1
[Direction]	31.9	33.6	32.4
[Latitude]	1.5	1.7	1.7
[Longitude]	1.7	1.7	1.8
Direction	− 5.6	3.8	3.0
Latitude	0.1	− 0.3	0.0
Longitude	0.2	0.0	− 0.3
S.D. Dist	72.0	67.6	66.8

P	Position	|Direction|
CPLR vs Persistence	.03	.25
AVM vs Persistence	.047	.32

Table 8
Recurring cyclones, four forecasts

Mean Position Error

97.4	CPLR
82.5	AVM
109.0	Persistence

Overall there appears to be little to choose between the methods. The CPLR and persistence mean position errors are slightly less than the AVM error but the standard deviations are larger. In both cases the sum of the mean error and one standard deviation is 171 nautical miles. The AVM position error was greater than this value on 22 occasions, on eight of which the CPLR error was greater still. The CPLR position exceeded 171 n mi on 26 occasions, on seven of which AVM was worse. The Wilcoxon test indicates that the differences are not significant at the 5% level. The closeness of the means might lead one to suppose that AVM and especially CPLR are merely reproducing the pure persistence forecasts. An inspection of the results of individual forecasts shows that this is not the case. For instance, the AVM and persistence errors for Felix at 2300 GMT on 25 December were 72 and 30 n mi respectively, and for Neil at 1100 GMT on 28 February were 12 and 52 n mi. The CPLR and persistence errors for Max at 2300 GMT on 17 March were 34 and 119 n mi respectively, and for Neil at 1500 GMT on 6 March were 72 and 13 n mi.

All three methods produce large errors when cyclones are at latitudes polewards of 20°S at forecast time but AVM appears to be superior to CPLR. The Wilcoxon test shows

that the differences are significant (just) at the 5% level. The AVM error is slightly less than the persistence error but the difference is not significant. The same remarks apply to eastward-moving cyclones, with the added observation that the standard deviation of persistence errors is larger (95.7 n mi) than that of either CPLR (83.6) or AVM (83.5), and the AVM direction forecasts are significantly better than both CPLR and persistence direction forecasts.

CPLR and persistence are not significantly different and are clearly superior to AVM when the cyclone is at a latitude equatorward of 20°S or westward-moving. All three methods do better with this category of cyclones relative to their own performance at higher latitudes or with eastward movement. Both AVM and CPLR did significantly better (at the 5% level) on those occasions when the persistence error was greater than its mean value, with CPLR being the better of the two. This suggests that the non-persistence components of both these methods are exhibiting skill with these 'difficult' tracks.

Pure persistence by definition cannot forecast recurvature, and CPLR cannot forecast recurvature in climatologically unusual positions. AVM was the best performer with

Figure 1 Forecast position for cyclone Neil produced by the CPLR and AVM methods, shown with the corresponding best-track positions. All positions are for 0500 GMT. The position numbered 1 is for February 26, 1981.
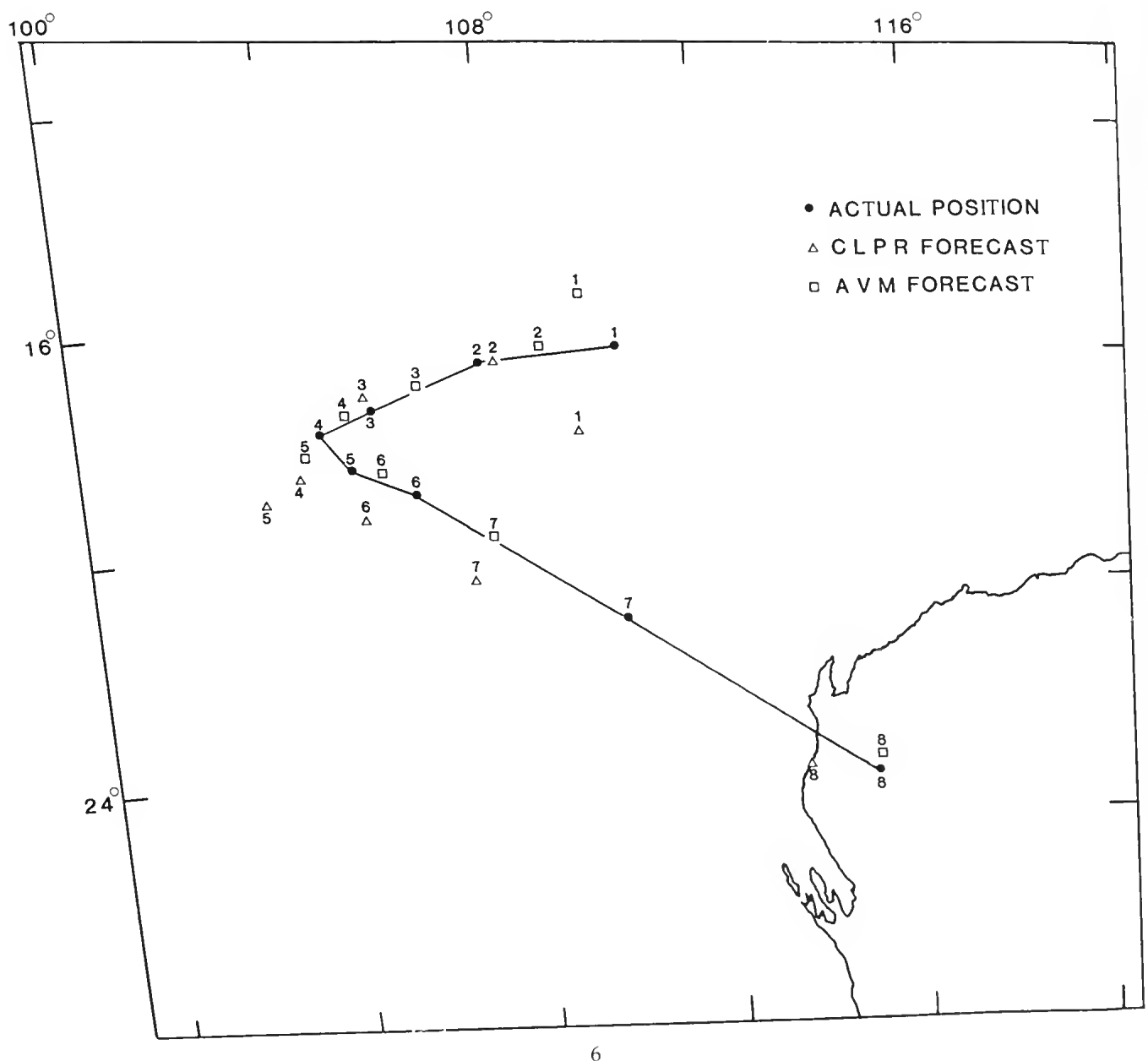
the four recurving cyclones (mean error 82.5 n mi) followed by CPLR (mean error 97.4 n mi) and persistence (mean error 109 n mi). The sample is too small to justify application of tests of significance. A sample result is displayed in Fig 1, which shows the track of cyclone Neil. Note that the CPLR and persistence forecasts tend to overshoot the point of recurvature whereas AVM more closely follows the best track.

Conclusions

If the cyclones in our sample are representative of cyclones in the Western Australian region then in most cases it would be difficult to improve on persistence 24-hour forecasts. This result was not entirely unexpected in view of the findings of Holland and Pan (1981) and Holland (1983, 1984) that tracks of west Australian cyclones are less variable than those of cyclones in the eastern Australian region. Both CPLR and AVM are better than persistence when the tracks are difficult in the sense that the error of a persistence forecast is worse than the mean persistence error. In view of the fact that AVM matched CPLR and persistence overall and in some categories surpassed them, and this occurs in spite of the handicaps previously described, we consider that it has exhibited some worth. It is likely to be most useful for cyclones in higher latitudes and for forecasting unusual behaviour which CLIPER-type methods cannot handle. We are also of the opinion that these results represent a lower bound on the accuracy of the method and it is expected that incorporation of the strength of the vorticity maximum into the forecasting rule would be a significant improvement, in spite of the difficulty of obtaining accurate measurements of this quantity.

References

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Bird assemblages in relation to habitat measures in Gregory National Park, Northern Territory.

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Abstract

At 142 sites in the northern half of Gregory National Park, Northern Territory, vegetation characteristics were measured, and topographic and environmental features recorded at the same time that bird species were recorded (February to March, 1986). One hundred and four bird species were recorded.

A broad relationship existed between bird distribution and the inter-related parameters of floristic composition and structure of the vegetation. Bird composition was related to habitat categories of mixed species forests on mesa escarpments or riverine environments, eucalypt woodlands on plains, and eucalypt low open-woodlands on mesa slopes. These broad relationships were distorted by habitat locations, however, because similar vegetation from the Bullita and Victoria River Crossing areas supported different bird species.

The plains habitats had a higher number of bird species per hectare than the riverine habitats and the mesa tops. The Brown Honeyeater was the most abundant species while the Peaceful Dove occurred in the most habitats. The survey method was time efficient and effective but there should have been a more even sampling of the different areas defined from photo-patterns. At least some species (e.g. raptors) were undersampled and this may have hampered interpretation.

Introduction

The classification of vegetation usually by structure or dominant species and, sometimes, subsequent mapping of vegetation units often precedes the investigation of fauna of an area. Frequently the vegetation communities are recorded and then the birds associated with them are listed (e.g. Kikkawa 1968, 1982; Kikkawa *et al.* 1981; Kikkawa & Webb 1967). More recently, vegetation communities have been defined using statistical techniques and then visited repeatedly to define the birds associated with them (e.g. Braithwaite 1985; Woinarski *et al.* 1988). A vegetation survey of Gregory National Park in the Victoria River district of the Northern Territory (Fig 1) provided the opportunity to look at bird assemblages and to test whether habitat characteristics determined their distribution. This is the first study of the relationship between birds and vegetation in the western part of the Northern Territory.

Methods

The area

The climate of this region is monsoonal with rain (618 - 813 mm annually) falling for up to five months (predominantly December - February). (Further details on climate are included in Bowman *et al.* 1988.) Much of the area, particularly at the north-eastern end, consists of steep tablelands and hills with shallow soils (Stewart 1970). Soils are deeper on the lower slopes and river flats where they are usually of cracking clay. The region (about 16˚S), with its predominantly low open woodland, falls in the transition zone between the taller denser forests and woodlands to the north and the more arid vegetation to the south (Gillison 1983).

Data collection

(i) Vegetation sampling

Landsat imagery at a scale of 1:250,000 was interpreted visually to produce a map of gross land types. From this, two representative areas of about 25 km2 were selected near Victoria River crossing (towards the north of the Park) and Bullita homestead (towards the centre) for intensive study. To classify the vegetation, 328 (100 m2) quadrats were placed (181 at Victoria River and 146 at Bullita) within
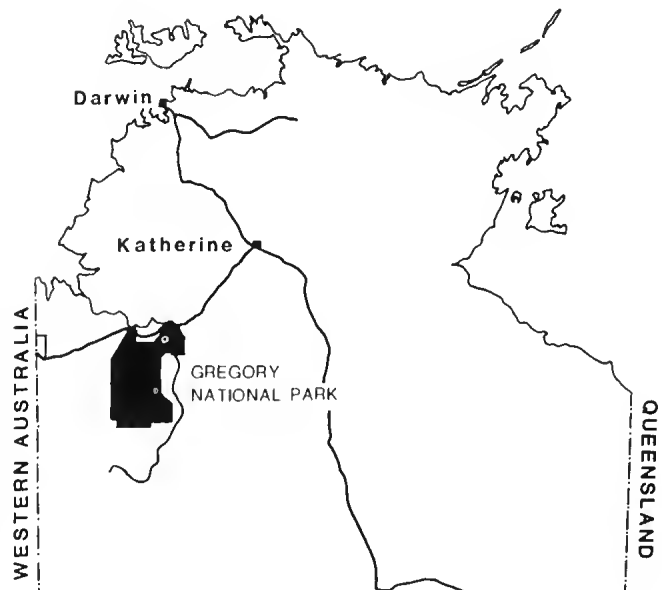

Figure 1. Map of the Northern Territory showing the location of Gregory National Park.

identified photo-patterns using a combination of systematic sampling of tracks, field traverse and helicopter landings during late February and early March 1986. Two teams, working in tandem, recorded all the vascular plant species in each quadrat, vegetation structure and major environmental parameters (topographic position, geology, soil texture, rock cover and slope). (The methods of the vegetation survey are reported more fully in Bowman *et al.* 1988.)

The subsequent numerical classification of the vegetation data identified 13 plant communities from the area near Victoria River crossing and 10 communities from the Bullita homestead area. The communities were found to be associated significantly with landform geology and could be grouped into landform complexes: riverine, plain, undulating terrain, and mesa plateau, slope or rim and escarpment (Table 1).

(ii) Bird sampling

One member (SCT) of one of the teams recorded the birds present at each site in about 100 m x 100 m, the area used to measure the basal area of the trees. This area included the vegetation quadrat and was perceived to be homogeneous with it. The area was searched thoroughly for about 15 minutes and presence of a species was scored on the basis of sight or call. Birds were censused throughout the day except between 1300 and 1400 h. Birds were conspicuous throughout the day because many were breeding.

Sampling was carried out at 142 sites which encompassed 20 of the 23 vegetation communities which were subsequently defined by floristic analysis. The number of bird sampling sites per vegetation community varied from 1 to 26.

Data analysis

The distribution of birds across the vegetation communities was considered in three ways.

(i) Comparison of sites by classification of bird species composition. Presence/absence of bird species from the 142 sites visited was stored on the ecological data base system Ecopak (Minchin 1986). Numerical analysis was carried out using the Numerical Taxonomy Package (NTP - Belbin *et al.* 1984).

The compositional similarity of sites was derived from the presence/absence lists of birds using the Bray Curtis association index. From this matrix the sites were clustered using the agglomerative hierarchical classification procedure WPGMA (Weighted Pair Group Mean Arithmetic), after the UPGMA (Unweighted Pair Group Mean Arithmetic) procedure was found to result in excessive 'chaining' with no clearly discernible groups. A dendrogram from the fusion table was generated. The final groups were then decided after examining bird species membership and their relationships with environmental parameters.

(ii) Comparison of vegetation communities by ordination of bird species composition. A parallel analysis was carried out to determine the relationship of the 20 vegetation communities, encompassed by the bird sampling, based on their bird species composition. Sites were agglomerated by vegetation unit to give percent frequency of bird species by vegetation unit. The relationship between the bird composition of the vegetation communities was portrayed by ordinating the 20 agglomerated sites using the Detrended Correspondence Analysis (DCA — Hill & Gauch 1980). The resulting ordination was related to vegetation and other environmental attributes.

Table 1

Summary of community number, structure, dominant plant species and topographic position of communities surveyed for birds, Gregory National Park, N.T. (after Bowman *et al.* 1988).

Community Number	Structure	Dominant Species	Mode Topographic Position
		Victoria River Area	
1	low open-woodland	*Eucaluptus dichromophloia, E. miniata, Plectrachne pungens*	mesa top
2	low woodland	*E. dichromophloia, Erythrophleum chlorostachys, P. pungens*	mesa top
3	woodland	*E. miniata, Terminalia latipes, P. pungens*	mesa rim and gully
4	forest	*Livistona sp. nova.*, mixed species	mesa gully
5	woodland	*E. tectifica, Lysiphyllum cunninghamii*, tall grasses	plain
6	low open-woodland	*E. tectifica, Er. chlorostachys*, tall grasses	plain
7	open-woodland	*E. tectifica, E. terminalis*, tall grasses	plain
8	low woodland	*Er. chlorostachys, E. tectifica, P. pungens*	mesa side
9	open-forest	*Strychnos lucida, Ziziphus quadriloculare*	mesa/ephemeral water course
10	low woodland	*Melaleuca argentea, Lophostemon grandiflorus*	riverine
11	woodland	*E. camaldulensis, Nauclea orientalis*	riverine
12	closed-forest	*M. symphiocarpa*	mesa gully
		Bullita Area	
14	woodland	*L. cunninghamii, E. tectifica, Adansonia gregorii, E. pruniosa*, tall grasses	plain
15	open-woodland	*L. cunninghamii, E. tectifica*, tall grasses	plain
16	low open-woodland	*E. brevifolia, P. pungens*	mesa side
17	low open-woodland	*E. dichromophloia, P. pungens*	mesa top
18	tall shrubland	*Acacia spp.*, tall grasses	variable
20	open-forest	*T. platyphylla, L. grandiflorus*, tall grasses	riverine
21	low closed-forest	*S. lucida, Celtis philipensis*	mesa rim
23	low open-woodland	*E. ferruginea, E. brevifolia, P. pungens*	mesa top

(iii) Comparison of feeding niche, species richness and habitat breadth.

Birds were classified on the basis of feeding niche (determined from numerous observations and Schodde & Tidemann 1986) and tested for association with the vegetation and bird groups. Birds were classed as aquatic [Q], raptorial [R], granivorous [S], insectivores — ground [G], feeders at flowers [B], insectivores — aerial [A], insect and fruit feeders [F], and insectivores — foliage [I].

Mean species richness for birds for each vegetation group was calculated if two or more bird sites were sampled from the group. Habitat breadth (B) measures were calculated for any species that was found in at least 3 of these communities using $B=1/(P_i^2)$, where P_i is the number of times a species occurs in vegetation unit i

divided by the total occurrences of the species over all vegetation units (Levins 1968). A comparison was made between the habitat breadths of birds recorded both in different habitat types near Darwin (Woinarski *et al.* 1988) and in this study. The correlation between the scores for birds in both habitats was calculated.

Results

A total of 104 bird species was recorded in the 142 samples (Table 2). Of these, 66 were recorded on more than four occasions. The most frequently observed species were the Brown Honeyeater (n=47), Peaceful Dove (n=46), Weebill (n=39), Mistletoebird (n=37) and Pied Butcherbird (n=36) (Table 2).

Table 2

Bird species recorded in the Victoria River and Bullita Areas of Gregory National Park, NT: sites with records of particular bird species expressed as a percentage of total sites (n) in each major plant community (vegetation/geological category) as defined by Bowman *et al.* 1988. The number of records of each bird species appears in brackets following its name. Feeding niche is defined as follows: Q = aquatic, R = raptorial, G = insectivore (ground), S = seed eater, B = feeders at flowers, I = insectivore (foliage), A = insectivore (aerial), F = insect and fruit feeder. Species richness and habitat breadth are defined in the text. Figures in brackets below habitat breadth figures are re-calculations of habitat breadth from Woinarski *et al.* (1988) for birds in the Darwin region.

Bird Species	Feeding Niche	Plant Communities (refer Table 1)								Habitat Breadth
		Mesa rim & escarpment		Riverine		Mesa Top		Plains		
		Victoria River Comm. Nos. 3, 9, 4, 12 n = 19	Bullita Comm. No. 21 n = 1	Victoria River Comm. Nos. 10, 11 n = 8	Bullita Comm. No. 20 n = 6	Victoria River Comm. Nos. 1, 2, 8 n = 34	Bullita Comm. Nos. 16, 17, 23 n = 5	Victoria River Comm. Nos. 5, 6, 7 n = 26	Bullita Comm. Nos. 14, 15, 18 n = 43	
Little Pied Cormorant (2) *Phalacrocorax melanoleucos*	Q			25						
Darter (1) *Anhinga melanogaster*	Q			12.5						
White-faced Heron (1) *Ardea novaehollandiae*	Q								2.3	
Black Kite (4) *Milvus migrans*	R			25		2.9		3.9		0.195 (5.69)
Whistling Kite (3) *Milvus sphenurus*	R								7.0	
Brown Goshawk (3) *Accipiter fasciatus*	R			12.5		2.9			2.3	0.373 (5.69)
Spotted Harrier (1) *Circus assimilis*	R								2.3	
White-bellied Sea-Eagle (1) *Haliaeetus leucogaster*	R			12.5						
Wedge-tailed Eagle (2) *Aquila audax*	R					2.9	20.0			
Brown Falcon (3) *Falco berigora*	R					2.9	20.0	3.9		0.259 (3.83)
Australian Kestrel (1) *Falco cenchroides*	R						20.0			
Peregrine Falcon (1) *Falco peregrinus*	R	5.3								
Brown Quail (2) *Coturnix ypsilophora*	S			12.5				3.9		
Chestnut-backed Button-quail (2) *Turnix castanota*	S							3.9	2.3	
Kori Bustard (1) *Ardeotis kori*	G								2.3	
Brolga (1) *Grus rubicundus*	Q							3.9		
Bush Thick-knee (1) *Burhinus grallarius*	G							3.9		
Crested Pigeon (8) *Geophaps lophotes*	S					2.9		3.9	14.0	0.376
Spinifex Pigeon (6) *Geophaps plumifera*	S			12.5		2.9			9.3	0.415
White-quilled Rock-Pigeon (1) *Petrophassa rufipennis*	S	5.3								
Bar-shouldered Dove (19) *Geopelia humeralis*	S		100	37.5	33.3	5.9	20.0	15.4	14	0.458 (9.23)
Diamond Dove (5) *Geopelia cuneata*	G	5.3				2.9		3.9	4.6	0.476

Table 2 (cont.)

Bird Species	Feeding Niche	Mesa rim & escarpment		Riverine		Mesa Top		Plains		Habitat Breadth
		Victoria River Comm. Nos. 3, 9, 4, 12 n = 19	Bullita Comm. No. 21 n = 1	Victoria River Comm. Nos. 10, 11 n = 8	Bullita Comm. No. 20 n = 6	Victoria River Comm. Nos. 1, 2, 8 n = 34	Bullita Comm. Nos. 16, 17, 23 n = 5	Victoria River Comm. Nos. 5, 6, 7 n = 26	Bullita Comm. Nos. 14, 15, 18 n = 43	
Peaceful Dove (46) *Geopelia placida*	S	10.5	100	50	83.3	26.5	40	46.2	25.3	0.716 (5.6)
Red-tailed Black-Cockatoo (5) *Calyptorhynchus banksii*	S			12.5	16.7		20		4.6	0.442
Cockatiel (5) *Leptolophus hollandicus*	S					2.9		3.9	7.0	0.320
Sulphur-crested Cockatoo (4) *Cacatua galerita*	S							11.5	2.3	
Little Corella (6) *Cacatua pastinator*	S			25				7.7	4.6	0.25
Galah (10) *Cacatua roseicapilla*	S					11.8		11.5	7.0	0.46
Rainbow Lorikeet (17) *Trichoglossus haematodus*	B			12.5	16.7	14.7		11.5	15.3	0.613 (6.36)
Varied Lorikeet (5) *Psitteuteles versicolor*	B				16.7			3.9	6.9	0.317
Red-winged Parrot (14) *Aprosmictus erythropterus*	S	10.5			50	2.9	20	3.9	14	0.373 (4.5)
Budgerigar (6) *Melopsittacus undulatus*	S					5.9		15.4		
White-cheeked Rosella (3) *Platycercus eximius*	S	5.3				2.9		3.9		0.422
Pallid Cuckoo (1) *Cuculus pallidus*	I								2.3	
Brush Cuckoo (4) *Cacomantis variolosus*	I				33.3				4.6	
Horsfield's Bronze-Cuckoo (8) *Chrysococcyx basalis*	I					5.9	20	3.9	9.2	0.426
Common Koel (5) *Eudynamys scolopacea*	I								12.3	
Channel-billd Cuckoo (1) *Scythrops novaehollandiae*	I							3.9		
Pheasant Coucal (6) *Centropus phasianinus*	I	5.3		12.5		2.9			7.0	0.399
Rufous Owl (1) *Ninox rufa*	R								2.3	
Southern Boobook (1) *Ninox boobook*	R					2.9				
Barking Owl (1) *Ninox connivens*	R							3.9		
Tawny Frogmouth (2) *Podargus strigoides*	G				16.7				2.3	
Fork-tailed Swift (1) *Apus pacificus*	A					2.9				
Blue-winged Kookaburra (14) *Dacelo leachii*	G		100	50		5.9	20	11.5	7.0	0.366 (6.35)
Sacred Kingfisher (10) *Todiramphus sanctus*	G				16.7	2.9	20	7.7	11.5	0.519 (3.63)
Red-backed Kingfisher (3) *Todiramphus pyrrhopygius*	G					5.9		3.9		
Azure Kingfisher (1) *Alcedo azurea*	Q				16.7					
Rainbow Bee-eater (26) *Merops ornatus*	A	5.3	100		33.3	17.7	80	19.2	16.1	0.505 (12.41)
Dollarbird (13) *Eurystomus orientalis*	A		100	25	33.3		20	15.4	7	0.385
Singing Bushlark (9) *Mirafra javanica*	G							3.9	18.4	
Black-faced Cuckoo-shrike (23) *Coracina novaehollandiae*	I	10.5				14.7	40	15.4	23	0.566 (7.33)
White-bellied Cuckoo-shrike (14) *Coracina papuensis*	I	5.3		37.5		8.8	20	11.5	7	0.465 (12.87)
White-winged Triller (32) *Lalage tricolor*	I	10.5			33.3	2.9	20	30.8	41.4	0.57
White-browed Robin (1) *Poecilodryas superciliosa*	I				16.7					
Lemon-bellied Flycatcher (1) *Microeca flavigaster*	I								2.3	
Jacky Winter (2) *Microeca leucophaea*	I				16.7				2.3	
Rufous Whistler (34) *Pachycephala rufiventris*	I	5.3	100		66.7	11.8	20	15.4	43.7	0.518 (3.78)

Table 2 (cont.)

Bird Species	Feeding Niche	Plant Communities (refer Table 1)								Habitat Breadth
		Mesa rim & escarpment		Riverine		Mesa Top		Plains		
		Victoria River Comm. Nos. 3, 9, 4, 12 n = 19	Bullita Comm. No. 21 n = 1	Victoria River Comm. Nos. 10, 11 n = 8	Bullita Comm. No. 20 n = 6	Victoria River Comm. Nos. 1, 2, 8 n = 34	Bullita Comm. Nos. 16, 17, 23 n = 5	Victoria River Comm. Nos. 5, 6, 7 n = 26	Bullita Comm. Nos. 14, 15, 18 n = 43	
Sandstone Shrike-thrush (4) *Colluricincla woodwardi*	I	21.1								
Grey Shrike-thrush (7) *Colluricincla harmonica*	I		100			2.9	20		9.3	0.191 (2.75)
Restless Flycatcher (9) *Myiagra inquieta*	I		100		50	2.9	20	3.9	4.6	0.299
Leaden Flycatcher (2) *Myiagra rubecula*	I	10.5								
Northern Fantail (4) *Rhipidura rufiventris*	I	21.1								
Willie Wagtail (13) *Rhipidura leucophrys*	G				33.3	2.9		3.9	20.7	0.299 (3.99)
Grey-crowned Babbler (31) *Pomatostomus temporalis*	G				16.7	11.8	20	19.2	46	0.492
Golden-headed Cisticola (11) *Cisticola exilis*	I							34.6	4.6	
Rufous Songlark (18) *Cinclorhamphus mathewsi*	I	5.3			16.7	14.7		19.2	14	0.563
Purple-crowned Fairy-wren (1) *Malurus coronatus*	I			12.5						
Variegated Fairy-wren (1) *Malurus lamberti*	I	5.3								
Red-backed Fairy-wren (17) *Malurus melanocephalus*	I	5.3				14.7		19.2	14	0.438 (8.78)
Weebill (39) *Smicrornis brevirostris*	I	31.6		50		38.2		46.2	9.2	0.538 (5.65)
White-throated Gerygone (6) *Gerygone olivacea*	I	10.5				2.9		7.7	2.3	0.378
Varied Sittella (5) *Daphoenositta chrysoptera*	I							7.7	7	
Black-tailed Treecreeper (9) *Climacteris melanura*	I				16.7	2.9	20	11.5	7	0.516
Silver-crowned Friarbird (29) *Philemon argenticeps*	B	31.6				47.1	20	23.1		0.442
Helmeted Friarbird (1) *Philemon buceroides*	B	5.3								
Little Friarbird (36) *Philemon citreogularis*	B	10.5		12.5		23.5	20	34.6	34.5	0.644 (3.31)
Blue-faced Honeyeater (12) *Entomyzon cyanotis*	B			25	33.3	5.9		7.7	9.3	0.435 (6.45)
Yellow-throated Miner (17) *Manorina flavigula*	B	5.3				14.7		3.9	23	0.47
Singing Honeyeater (12) *Lichenostomus virescens*	B						60	3.9	20.7	
White-gaped Honeyeater (8) *Lichenostomus unicolor*	B		100	25			20	7.7	4.6	0.26 (4.03)
Yellow-tinted Honeyeater (31) *Lichenostomus flavescens*	B	5.3			50	14.7	80	15.4	32.2	0.541
Black-chinned Honeyeater (2) *Melithreptus gularis*	B							7.7		
White-throated Honeyeater (9) *Melithreptus albogularis*	B	15.8		25		8.8		3.9		0.37 (2.42)
Brown Honeyeater (47) *Lichmera indistincta*	B	63.2		12.5	16.7	67.7	20	19.2	9.2	0.528 (12.81)
Bar-breasted Honeyeater (5) *Ramsayornis fasciatus*	B	5.3	100			5.9			2.3	0.16
Rufous-throated Honeyeater (16) *Conopophila rufogularis*	B		100		16.7		20		29.9	0.284 (2.21)
Banded Honeyeater (17) *Certhionyx pectoralis*	B	31.6				17.7		7.7	6.9	0.364
Mistletoebird (37) *Dicaeum hirundinaceum*	F	36.8	100	12.5		32.4	40	30.8	16.1	0.58 (5.84)
Red-browed Pardalote (4) *Pardalotus rubricatus*	I	5.3			16.7		20		2.3	0.364
Striated Pardalote (12) *Pardalotus striatus*	I	5.3		37.5		14.7		7.7	2.3	0.334 (8.63)
Crimson Finch (1) *Neochmia phaeton*	S							3.9		
Double-barred Finch (14) *Taeniopygia bichenovii*	S	5.3		12.5		14.7		7.7	11.5	0.564
Masked Finch (4) *Poephila personata*	S				16.7				7	

Table 2 (cont.)

Bird Species	Feeding Niche	Mesa rim & escarpment		Riverine		Mesa Top		Plains		Habitat Breadth
		Victoria River Comm. Nos. 3, 9, 4, 12 n = 19	Bullita Comm. No. 21 n = 1	Victoria River Comm. Nos. 10, 11 n = 8	Bullita Comm. No. 20 n = 6	Victoria River Comm. Nos. 1, 2, 8 n = 34	Bullita Comm. Nos. 16, 17, 23 n = 5	Victoria River Comm. Nos. 5, 6, 7 n = 26	Bullita Comm. Nos. 14, 15, 18 n = 43	
Long-tailed Finch (3) *Poephila acuticauda*	S						40		2.3	
Pictorella Mannikin (1) *Heteromunia pectoralis*	S					2.9				
Olive-backed Oriole (7) *Oriolus sagittatus*	F				33.3				11.5	
Great Bowerbird (24) *Chlamydera nuchalis*	F	36.8	100		16.7	8.8	20	3.9	23	0.444
Australian Magpie-lark (29) *Grallina cyanoleuca*	G				16.7	8.8		34.6	34.5	0.486 (4.71)
Black-faced Woodswallow (28) *Artamus cinereus*	A	5.3				17.7	60	26.9	25.3	0.511
Little Woodswallow (8) *Artamus minor*	A						40	3.9	11.5	0.242
White-breasted Woodswallow (2) *Artamus leucorhynchus*	A								4.6	
Pied Butcherbird (36) *Cracticus nigrogularis*	G	10.5		12.5	16.7	38.2	20	15.4	32.2	0.684 (5.4)
Torresian Crow (13) *Corvus orru*	G			25		8.8		11.5	11.5	0.421
Total Number Species (104)		36	13	28	31	54	34	63	72	
Mean Species Richness per quadrat (100 m x 100 m)		5.7	—	1.9	8.8	6.0	4.8	8.0	8.0	

Comparison of sites by classification of bird species composition

The dendrogram of the similarity of bird species composition of the 153 sites is shown in Fig 2. After inspection of bird species membership and associated habitat parameters it was decided to truncate the dendrogram at a dissimilarity of 1.6 which resulted in 7 bird groups.

By grouping vegetation communities with similar habitat characteristics, broad relationships were established between bird group and habitat (mesa rim, riverine, mesa top and side, and plains) and area (Bullita or Victoria River) (Table 3). The proportions of birds assigned to particular food niches for each of the bird groups obtained from the dendrogram (Table 4) can be related to the group structures in Table 3.

Group 1 (Table 3) was significantly associated with riverine habitats at Bullita. Birds from this group comprised seed eaters and ground insectivores (Table 4) and commonly included the Yellow-tinted Honeyeater, Peaceful Dove, Pied Butcherbird and Black-faced Cuckoo-shrike.

Group 2 was significantly associated with the plains communities at Bullita and Victoria River with only minor occurrences in other habitats. There was a high proportion of foliage gleaners (insectivores) including the Singing Bushlark, Golden-headed Cisticola and Yellow-throated Miner.

Group 3 was significantly associated with riverine habitat at Victoria River where it was more extensive than that at Bullita. Foliage insectivores as well as seed eaters were
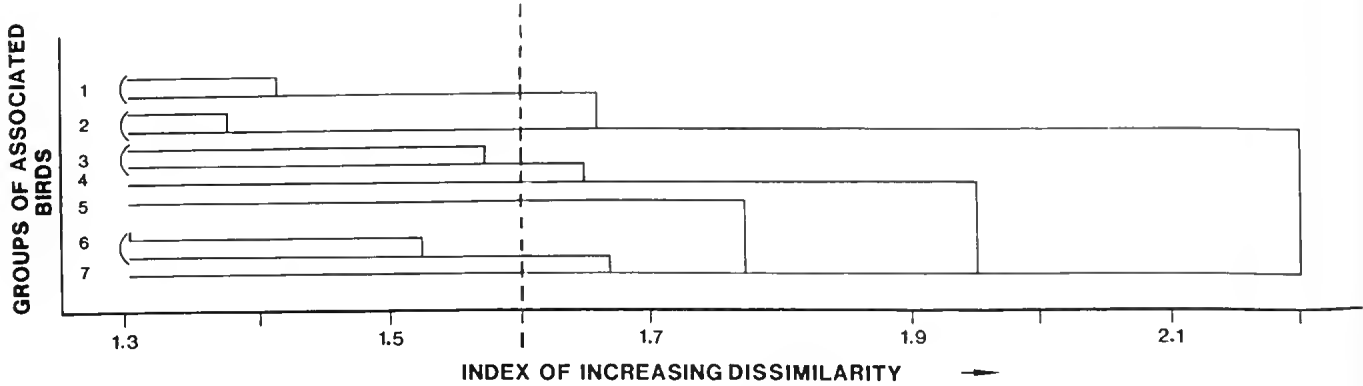
Figure 2. Dendrogram showing the relationship between bird presence/absence samples at the 7 group level using the Bray Curtis similarity measure and the WPGMA sorting strategy.

most commonly found and included the White-bellied Cuckoo-shrike, Peaceful Dove and Bar-shouldered Dove.

Group 4 was significantly associated with the mesa tops at Bullita, where *Grevillea angulata* bushes were commonly in flower, but also on the plains there. The feeding groups most frequently occurring were the fruit and insect eaters, the aerial insectivores and the feeders at flowers and were represented by the Great Bowerbird, Mistletoebird, Rainbow Bee-eater, Little Woodswallow and Singing Honeyeater.

Groups 5 and 7 were both significantly associated with the closed forest communities on the mesa rims and escarpments at Victoria River, with group 5 also occurring on the mesa tops there, with their floristically and structurally distinct open-woodlands. These groups comprised feeders at flowers and were characterized by the Brown Honeyeater, Silver-crowned Friarbird and Rainbow Lorikeet.

Table 3

Association between groups of related birds (from dendrogram, Fig 2) and the vegetation and topography of Gregory National Park, NT. (Numbers in brackets are the plant communities from Table 1).

Vegetation, Geology and Topography		Groups of related birds							No. birds
		1	2	3	4	5	6	7	
Mesa Rims & Escarpments	Victoria River (3,4,9,12)	0	0	1	1	9 ***	5	3	1
	Bullita (21)	0	0	1	0	0	0	0	3
Riverine	Victoria River (10,11)	1	0	5 ***	0	1	1	0	0
	Bullita (20)	3 ***	1	2	0	0	0	0	1
Mesa Top	Victoria River (1,2,8)	4	3	3	0	12 ***	10	2	2
	Bullita (16,17,18,23)	2	1	1	3 ***	0	1	0	3
Plains	Victoria River (5,6,7)	2	9	3	0	2	8	2	1
	Bullita (14,15)	7	24	3 ***	4	2	0	0	0
		19	38	19	8	26	25	7	11

*** significant associations (P < 0.05) using one sample chi-square analysis

Group 6 was not associated with any particular habitat although it was found on the mesa tops and plains at Victoria River and was characterized by the foliage gleaning Weebill.

Comparison of vegetation communities by ordination of bird species composition

The ordination of the percent occurrence of birds by the 20 vegetation communities is presented graphically in Fig 3. On the same diagram the habitats are identified as occurring at Bullita or Victoria River and as mesa, plain, riverine or hill. Those communities on mesas are subdivided further into top, side-slope, rim or ephemeral watercourses. The communities are enveloped into gross vegetation/landform/area types where appropriate to aid interpretation.

Superimposed on the diagram are values of percent foliage cover of the upper stratum and floristic DCA 1 score from the first axis (taken from Bowman *et al.* 1988).

Broad quantitative relationships between the vegetation parameters of foliage cover and floristic composition as measured by the floristic DCA 1 score (from Bowman *et al.* 1988) are apparent. (The floristic DCA 1 score was related to topographic position through its influence on moisture status.) Generally habitats with high DCA 1 and DCA 2 scores were associated with vegetation communities with high floristic DCA 1 scores, which represents high moisture status and associated high canopy covers. Habitats with low DCA 1 and DCA 2 scores had low floristic DCA 1 scores, indicating drier sites and associated low canopy covers.

There was also a clear differentiation between habitats from the Bullita area which generally had low DCA 1/high DCA 2 scores and those from the Victoria area which had high DCA 1/low DCA 2 scores. This trend over-rode the relationship between the floristic and structural characteristics and bird composition. For example, the sites from mesa rims at Bullita (community 21) and Victoria River were floristically and structurally distinct from other plant communities due to the increased moisture run-off associated with the habitat. The bird composition in the vegetation of the Bullita mesa rim was more similar to that in the floristically different sites on the mesa tops (community 16) than to the floristically and structurally similar vegetation types at Victoria River (communities 3, 4 and 12). The riverine communities show a wide variation in composition of bird assemblages but the sample sizes per community were low (10: n=1, 11: n=7).

Comparison of feeding niche, species richness and habitat breadth.

Granivores [S] (n=21) and species feeding on insects in shrubs and trees [I] (n=29) were the most common (Table 1). Only 3 of the 8 niche groups showed significantly

Table 4

Mean proportions (%) of birds assigned to particular food niches compared with groups of affiliated birds (from dendrogram Fig 2). Within a column, the letters a, b, and c indicate the means that do not differ from each other at P=0.05 level using SNK test.

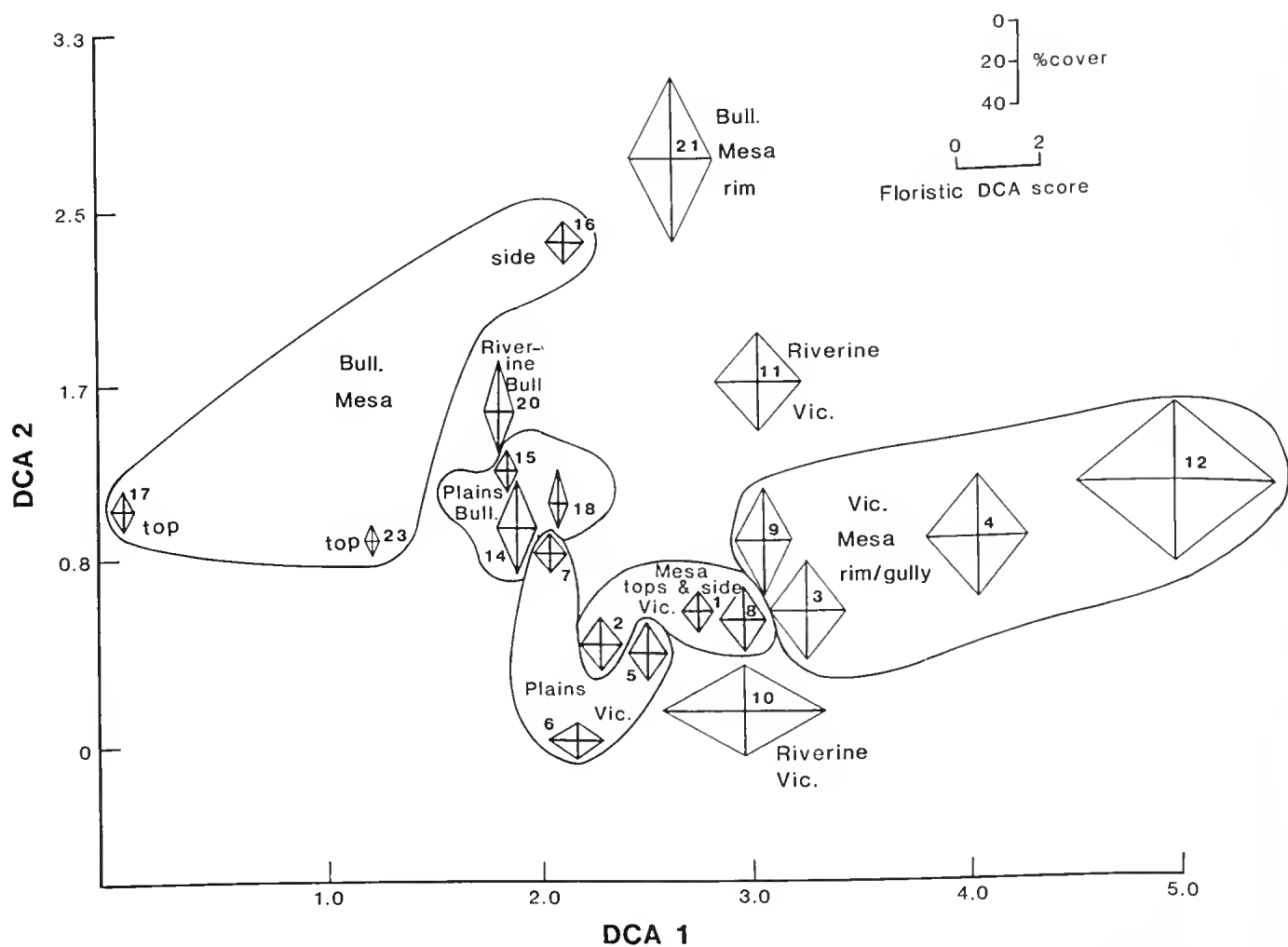| Bird Groups	Aquatic	Raptorial	Seeds	Insects (ground)	Flowers	Insect (aerial)	Fruit/insects	Insects (foliage)
1	0.2	3.4	28.8a	20.0a	24.1b,c	9.4b	1.9c	16.7b
2	0.3	2.7	13.1c	16.1a,b	22.6c	6.8b	4.9c	33.6b
3	2.6	4.1	29.6a	7.2c	18.1b,c	7.3b	3.3c	27.8b
4	—	0.8	5.6c	—	22.4b,c	20.9a	31.9a	18.4b
5	—	2.1	9.4c	7.7c	45.6b	1.1b	8.8c	25.3b
6	—	1.8	12.7a,b	6.5c	13.8b,c	4.8b	16.3a,b	39.3a
7	—	—	3.6c	4.1b,c	66.2a	—	12.0b,c	14.1b
	n.s.	n.s.						

Figure 3. Detrended Correspondence Analysis (DCA) ordination of bird species grouped according to the vegetation/ landform classification of Bowman *et al.* (1988). (The floristic DCA scores and % canopy cover from Bowman *et al.* have been superimposed on the bird DCA scores; the heights of the diamonds represent % canopy cover of dominant layer; widths of diamonds represent the floristic DCA score; Vic.= Victoria River crossing region (towards north-eastern end), Bull.= (more central) Bullita region, of Gregory National Park, Northern Territory.)

Table 5

Mean proportions (%) of birds assigned to particular food niches compared with bird groups sorted according to vegetation categories of Bowman *et al.* (1988). Within a column, the letters a and b indicate means that do not differ from each other at P=0.05 using SNK test.

Location	Aquatic (n=5)	Raptorial (n=12)	Seeds (n=21)	Insects (ground) (n=12)	Flowers (n=16)	Insects (aerial) (n=6)	Fruit/insects (n=3)	Insects(foliage) (n=29)
				Feeding Niche				
				Mesa Rims + Escarpments				
Vic.	0	0.8	6.1b	33.5a	38.1	5.1	19.6b	33.5
Bullita	0	0	15.4a,b	23.1a,b	23.1	15.4	15.4a,b	23.1
				Riverine				
Vic.	1.2	0	36.0a	24.4a,b	14.8	2.0	2.5a,b	24.4
Bullita	0	0	27.1a,b	30.3a,b	18.6	8.5	5.7a,b	30.3
				Mesa Tops				
Vic.	0	3.3	12.5b	10.3b	36.0	7.5	8.5a,b	26.2
Bullita	0	6.7	10.7b	34.4a	18.0	17.7	7.0a	23.7
				Plains				
Vic.	1.8	2.4	19.7a,b	30.6a	21.4	6.3	4.3a	30.6
Bullita	0.1	2.0	14.3b	27.5a	27.2	8.0	11.7a,b	33.8
	n.s.	n.s.			n.s.	n.s.		n.s.

different proportions when sorted according to the vegetation categories (Table 5). These were the seed eaters which were most abundant in riverine habitat, and both ground feeding insectivores and fruit eaters which were most abundant in the plains vegetation (Table 5). A stronger association occurred when the same feeding categories were compared with the groups of birds derived from the dendrogram (Table 4) as described above. Fruit-eaters were

Table 6
Number of communities supporting birds when they are clumped according to feeding niche.

Feeding Niche	Mean no. of communities	Standard deviation
Seed eaters (S) (n=21)	3.3	1.9
Insect gleaners (I) (n=29)	3.2	2.0
Aquatic (Q) (n=5)	1.0	0
Raptorial (R) (n=12)	1.6	0.9
Ground insectivores (G) (n=12)	3.7	2.0
Aerial insectivores (A) (n=6)	3.8	2.6
Flower feeders (B) (n=16)	4.2	1.6
Fruit & insect feeders (F) (n=3)	5.3	2.9

found in more communites (mean=5.3; s.d.=2.9) than other groups (Table 6). The least widely distributed were the aquatic and raptorial species (Table 6).

The mean species richness per hectare was calculated for 7 habitats and ranged from 1.9 (riverine at Victoria River) to 8.8 (riverine at Bullita) (Table 2). Overall the plains habitat was the richest in species with an average of 8.0 per hectare compared with 5.4 for mesa tops and riverine habitats (Table 2). Where habitat breadths were calculated, they ranged from 0.16 (Bar-breasted Honeyeater, recorded 5 times) to 0.716 (Peaceful Dove); the most common species (Brown Honeyeater) had a habitat breadth of 0.53 (Table 2). For those species also occurring in the Darwin region, the re-calculations from Woinarski *et al.* (1988), ranged from 2.42 for the White-throated Honeyeater to 12.87 for the White-bellied Cuckoo-shrike.

There were 27 species that were recorded in both the Darwin region and three or more times in this study (Table 1). There was a significant positive correlation between the habitat breadths in both regions (r_s=0.67, n=27, p<0.001).

Discussion

Some of the birds recorded here were seen infrequently. For example, raptors and aquatic species are large birds with large home ranges and may have been undersampled using the method above. In addition, some birds are seasonally nomadic in the Top End of the Northern Territory (the raptors); are nocturnal; are restricted to certain habitats (rock-pigeon, Sandstone Shrike-thrush, Purple-crowned and Variegated Fairy-wrens, Crimson Finch); are migratory (Channel-billed Cuckoo); or, were in areas that were sampled infrequently (the aquatic species).

The topography as well as floristics and vegetation structure were correlated with the distribution of the birds. For example, birds that were found on the plains were found also on the adjacent low hills even though they differed floristically; and bird communities on the mesa tops and sides were similar to some of those in the closed forest on adjacent escarpments even though the vegetation was floristically and structurally distinct. This could be expected given the mobility of birds and also the opportunistic attraction by some (e.g. honeyeaters, woodswallows, lorikeets) to flowers in general rather than flowers of a particular species.

The contrast between the riverine habitat and non-riverine was greater at Bullita which is drier than at Victoria River. This could account for the riverine species richness at Bullita being more than 4 times greater than at Victoria River. The plains may have been the richest of all the habitat types recorded in this study because they were more extensive and so have developed a larger avifauna over time. This is reflected in the plant communities of the Top End where the savannah woodlands are the richest in terms of plant species number (Bowman *et al.* 1988a). The most frequently recorded bird species, the Brown Honeyeater, was not the most widely distributed across vegetation types. The Peaceful Dove was the characteristic species of the general region.

From the comparison of the habitat breadths of birds common to the Darwin region (from Woinarski *et al.*) and Gregory National Park, it appears that each individual species will behave in the same broad way to using habitat even though the floristics and structure may vary.

There were distinct gradients in the distribution of birds that reflected the climatic, topographic and vegetation differences between the drier, more open landscape of Bullita and the steeper escarpment country at the Victoria River end. For example, there is a better representation of raptors, parrots and acanthizids in the Victoria River area. The differences may have been better defined if numbers of individuals rather than just presence had been recorded. Any future survey should be designed to overcome this.

Classifying individual samples by bird composition produced groups that had gross associations with habitat. These bird/habitat patterns were better defined when bird composition was averaged within vegetation groups because it was found, with a few exceptions, that similar vegetation types had similar bird composition.

To improve this survey method, samples should be more evenly distributed among the categories defined on the aerial photographs during the initial planning stage. The problem of sampling within 'perceived' habitat types was overcome because the maximum number of areas discernible on the landsat images were sampled. By using one observer for all bird samples, the variability due to observer bias was minimized (compared with Friend & Dudzinski 1981; Block *et al.* 1987). The reliability of any survey can be increased with larger samples. The number of samples varies between studies from 1000 (Woinarski *et al.* 1988) to 13 areas (and undefined number of samples) (Kikkawa *et al.* 1981). Repeated sampling would define differences that might arise because of seasonal variation. As in the case of this study, a pre-determined 'one off' census, birds should be recorded at a time when the maximum number of species typical of the area is likely to be present. The survey methods used in this study satisfied the aims of the study and are appropriate if time-efficient surveys are required especially in areas that have never been studied before.

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Host preferences of Paropsini (Coleoptera: Chrysomelidae) in south-western Australia

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Abstract

The paropsine beetles *Chrysophtharta debilis* and *Paropsis elytrura* respectively showed distinct preferences for a Symphomyrtus species of Eucalyptus, *E. rudis*, and a Corymbia species, *E. calophylla*. Female beetles of both species laid more eggs on their preferred host and, while larvae of both species matured more rapidly on *E. rudis*, *C. debilis* did so faster than *P. elytrura*. *Eucalyptus marginata* was a poor host in terms of female oviposition and larval survival.

Introduction

Eucalypts in Australia are attacked by a wide range of leaf-eating insects, including phasmatids (Shephard 1957), sawflies (Carne 1965) and Lepidoptera (Campbell 1962). Indigenous paropsine beetles and their larvae are also prominent defoliators of eucalypts (Carne 1966), but are normally present at low or moderate population levels. Outbreaks have occurred, however, leading to defoliation over extensive areas and loss of growth in individual trees (Greaves 1966). The species *Paropsis charybdis* Stal has also caused serious damage to eucalypt plantations in New Zealand (Carne 1966).

Published biological information concerning paropsines is limited to species from eastern Australia (Cumpston 1939, Carne 1966, Tanton & Elipa 1978) and Tasmania (de Little 1979, Kile 1974). There are no published papers on paropsines from Western Australia, despite the fauna being rich in species. Two of the most widely distributed and locally abundant paropsines are *Chrysophtharta debilis* Chapius and *Paropsis elytrura* Blackburn. These species are found alone on small trees and coppice, or in association with other species of paropsines. Both species have also been observed damaging planted eucalypts on road verges and farm trees (G Hall, unpublished observations)

This paper describes a laboratory trial designed to quantify observed field preferences for host trees. The two species here selected have similar behaviour and distribution as other paropsines in southwestern Australia.

Methods

Study area

Studies were carried out at Helena Valley, 30 km east of Perth. The study area supported 1-3 m tall regrowth stands of *Eucalyptus calophylla* R.Br. ex Lindley (Corymbia), *Eucalyptus marginata* Donn ex. Smith (Monocalyptus) and *Eucalyptus rudis* Endl. (Symphomyrtus).

Oviposition preference

Two pairs each of adult *C. debilis* and *P. elytrura* were randomly selected from a culture stock and placed in separate plastic boxes (18 x 12 x 4 cm), and maintained at 23°C and 14 hours photophase. Matched cut shoots of *E. calophylla*, *E. marginata* and *E. rudis* were placed in water-filled, stoppered glass vials and a shoot of each species placed in each box. Shoots were replaced every 2-3 days. Numbers of eggs laid on the shoots by each species were tallied over 6 weeks. At the end of the trial all beetles remained alive.

Feeding trial

Thirty cultures each consisting of 20 larvae were established in plastic rearing boxes (18 x 12 x 4 cm) such that there were five replicates of each beetle species on each eucalypt species. Cultures were established from day-old larvae which had consumed their egg shells, and were maintained at 23°C and 14 hours photophase. Every 2-3 days surviving larvae were transferred to clean boxes containing fresh, young foliage. The foliage was taken from a few trees, selected for phenotypic similarity. The shoots were matched for uniformity of size and leaf texture. When mature, the larvae dropped to the floor of the box, and were weighed within 24 hours.

Results

Oviposition preference

The total number of eggs laid by both species on each host is shown in Table 1. Chi-square analysis shows that the data are heterogeneous (P<0.001), indicating an ovipositional preference of *C. debilis* for *E. rudis* and *P. elytrura* for *E. calophylla*. Both species oviposited least on E. marginata.

Feeding trial

Both species survived poorly on *E. marginata*, with only one *P. elytrura* larva surviving to maturity. This host species was therefore omitted from the statistical analysis. Larvae of both species survived to maturity on *E. calophylla* and *E. rudis* (Table 2). *C. debilis* showed a significantly better survival (P<0.001) on *E. rudis*, whereas *P. elytrura* survived best on *E. calophylla*.

Table 1

Number of eggs desposited by two females each of *C. debilis* and *P. elytrura* on shoots of *E. calophylla*, *E. marginata* and *E. rudis* in the laboratory over a six week period.

Species	E. calophylla	E. marginata	E. rudis
C. debilis	182	50	908
P. elytrura	1344	160	772

	E. calophylla	E. marginata	E. rudis	Sig.[2]
	% Survival ± SE[1]			
C. debilis	17 ± 9.8	0	78 ± 6.9	***
P. elytrura	84 ± 4.8	1 ± 1	17 ± 4.6	***
	Mean duration of larval stage (days) ± SE			
C. debilis	17.7 ± 0.9	—	14.0 ± 0.2	*
P. elytrura	23.9 ± 0.1	20	22.5 ± 1.0	NS
	Mean mass (mg) ± SE			
C. debilis	50.1 ± 1.6	—	50.0 ± 0.9	NS
P. elytrura	157.4 ± 4.2	131.5	113.4 ± 9.4	*

[1]Means of five replicates
[2]Only relates to comparison between *E. calophylla* and *E. rudis*: ***P<0.001, *P<0.05

Larvae of both species developed fastest on *E. rudis*, with the *C. debilis* - *E. rudis* combination being the most rapid. Mature larvae of *P. elytrura* achieved a greater mass on *E. calophylla* (P<0.05) than on *E. rudis*, whereas the weight of *C. debilis* larvae was similar between these two hosts.

Discussion

Of the most common species of paropsines occurring in mixed associations, *C. debilis* and *P. elytrura* respectively showed distinct host preferences to the Symphomyrtus species, *E. rudis*, and to the Corymbia species, *E. calophylla*. These results are in agreement with Burdon and Chilvers (1974) and de Little and Madden's (1975) findings that various paropsines show preferences for particular Eucalyptus subgenera. The current data are first report of a paropsine preferring a Corymbia species.

Females of *C. debilis* and *P. elytrura* showed an ovipositional host preference, indicating their role in the selection of preferred hosts. The larvae of both species survived better and grew larger on the host that the females preferentially selected.

This study has shown that *E. marginata* is a poor host for paropsines. Both beetle species laid fewer eggs on *E. marginata* and only one of 200 larvae survived to maturity. This result agrees with Majer and Recher (1988) who reported that *E. marginata* had a significantly lower invertebrate population than *E. calophylla* or *E. wandoo*.

The potential for population outbreaks of *C. debilis* and *P. elytrura* in south-western Australia appears low due to the eucalypt hosts occurring in mixed stands, even after logging. This contrasts with the situation in Tasmania where the preferred Monocalyptus host of *Chrysophtharta bimaculata* (Olivier) forms pure regrowth stands in which severe outbreaks occur (de Little & Madden 1975).

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Rhythmic igneous layering from the Gilgarna Rock syenite, Yilgarn Block, Western Australia

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Abstract

A rare example of rhythmic igneous layering from the felsic alkaline suite of the eastern Yilgarn Block occurs at Gilgarna Rock. Features of the layering, and the general petrographic character of the rocks, are consistent with production of the layering via the influence of an exsolved aqueous fluid. Depletion of fluorine within the melt is believed to have facilitated production of the aqueous fluid. Cyclic variations in fluid pressure are thought to have resulted in alternating pyroxene-feldspar crystallization, leading to the development of the rhythmic layering. Development of sedimentary-type structures indicates minor modification of the original layering, possibly via the current action of fluid movement during pressure release.

Introduction

Rhythmic igneous layering is characterized by pronounced systematic repetition of distinctive layers or sequences of layers, on scales varying from centimetres to metres. Rhythmic layering has been attributed to a number of processes, including crystal settling, convection and density grading (Wager & Brown 1968); liesegang-type growth (McBirney & Noyes 1979) and *in-situ* microrhythmic differentiation (Boudreau 1987), involving processes of crystal nucleation, resorption, coarsening, and chemical diffusion; and shifts in phase equilibria controlled by fluid exsolution due to the action of fluxing components (Rockhold *et al.* 1987). Such layering commonly occurs within mafic intrusions of low viscosity and high diffusivity, however, it is comparatively rare within felsic intrusions, particularly silica-oversaturated examples, where relatively low temperatures and high viscosities inhibit the development of layering (Emeleus 1963; Urbain *et al.* 1982; Rockhold *et al.* 1987).

One of the few examples of rhythmic layering in felsic intrusions within the Yilgarn Block, and the only example observed in a regional study of the felsic alkaline suite, occurs within the Eastern Goldfields Province of the Yilgarn Block at Gilgarna Rock, 103 km east-northeast of Kalgoorlie (Fig 1).

Geological setting

The syenites comprising Gilgarna Rock display mesoperthitic alkali feldspars, alkali pyroxenes and amphiboles, and low quartz contents typical of the felsic alkaline suite of Libby (1978).

A medium grained phase is intruded by a mineralogically and geochemically similar coarse grained phase, with recent Rb-Sr whole-rock and mineral dating (Johnson & Cooper 1989) establishing crystallization ages of 2627 ± 41 Ma and 2542 ± 14 Ma, respectively. The contact between the two phases is sharp, and sub-vertical rhythmic layering is observed within the younger coarse grained phase parallel
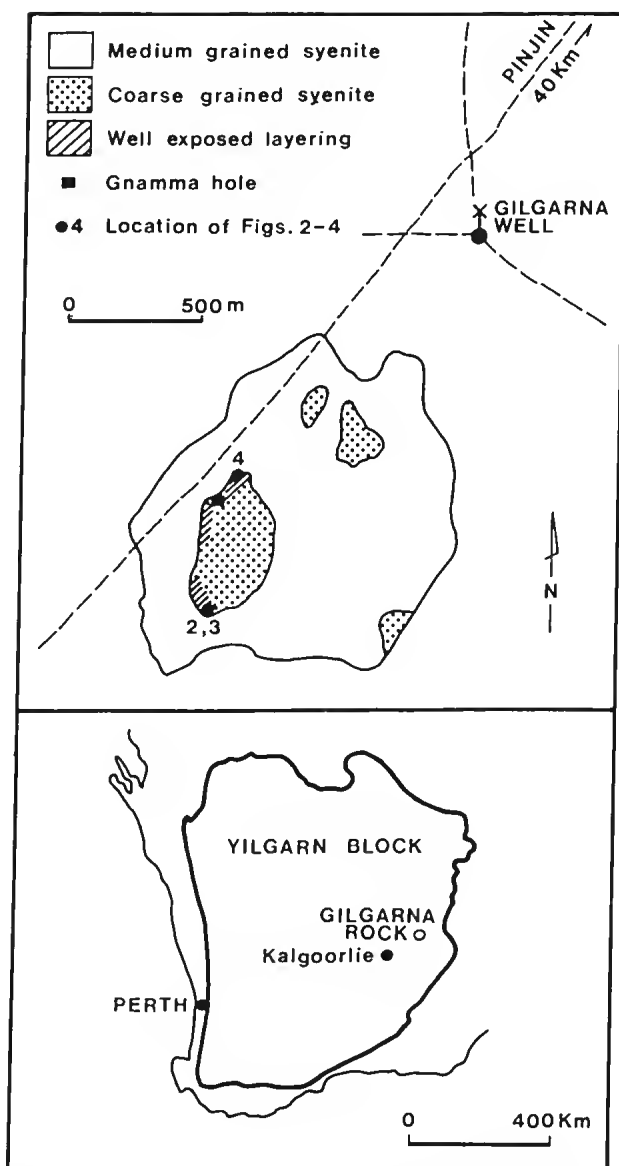
Figure 1 Location diagram and geological sketch, Gilgarna Rock.

to, and for distances of 1-5 m from, the contact. The layering is microrhythmic in form, often termed inch-scale layering (Hess 1960), and is defined by alternating predominantly mafic and predominantly felsic layers (Figs 2 & 3). Individual layers exhibit thicknesses of 0.5-15 cm, with minor pinching and swelling, and can be traced along strike for distances of up to 10 m.

Mafic layers are composed primarily of zoned alkali pyroxenes (>70%), with augite to aegirine-augite cores surrounded by aegirine-augite rims; feldspar (<20%), predominantly oligoclase to albite, with minor mesoperthite to antiperthite; titanite (5%); quartz (5%), usually as a late-stage interstitial phase; and accessory apatite and magnetite. Minor late alteration of alkali pyroxene to magnesioriebeckite is also present.

Felsic layers consist predominantly of feldspar (>80%), with medium to coarse grained oligoclase to albite and mesoperthite to antiperthite, and a mineralogically identical finer grained component with up to 10% quartz. Zoned augite/aegirine-augite (<20%) and trace titanite are the other constituents.

Elsewhere within the coarse phase syenite, oligoclase-albite occurs only as rare remnant cores to alkali feldspars. The common occurrence of oligoclase-albite in the felsic layers described above reflects early feldspar precipitation; with continued cooling, plagioclase moves down the solidus surface and is eventually replaced by anorthoclase as the crystallizing phase (Carmichael *et al.* 1974). Sub-solidus unmixing of anorthoclase leads to the development of mesoperthite to antiperthite.

Within both types of layers, occasional very thin layers of the other type occur, almost down to single-crystal scale in some cases. There is no indication of density grading within individual layers, and no relationship between layer spacing and crystal grainsize. Contacts between the rhythmic layers are generally sharp, although there are some rather diffuse examples. Sedimentary-type features within the layering are common, and include scour and fill structures, cross bedding, disrupted and slumped blocks, indistinct features approaching flame structures in form, and small-scale syn-crystallization microfaults (Fig 4). In addition, orbicular structures up to 0.75m long by 0.5m wide are present, with margins defined by concentrations of mafic minerals up to 30mm in thickness. All facing criteria suggest the influence of currents towards the contact of the medium grained phase, that is, away from the interior of the coarse grained phase.

Evidence of autometasomatism at Gilgarna Rock includes albite rimming of early mesoperthitic feldspars, aegirine-rich rimming of augite/aegirine-augite, partial replacement of pyroxene by magnesioriebeckite, and trace patchy colourless mica and fluorite replacement of feldspar. These autometasomatic products are best developed towards the margins of the coarse phase, and in the immediately adjacent medium phase.

Discussion

The lack of crystal sorting or density grading within individual layers at Gilgarna Rock argues against the major influence of crystal settling and convection processes on the

Figure 2 Microrhythmic (inch-scale) layering within the coarse phase syenite, Gilgarna Rock.
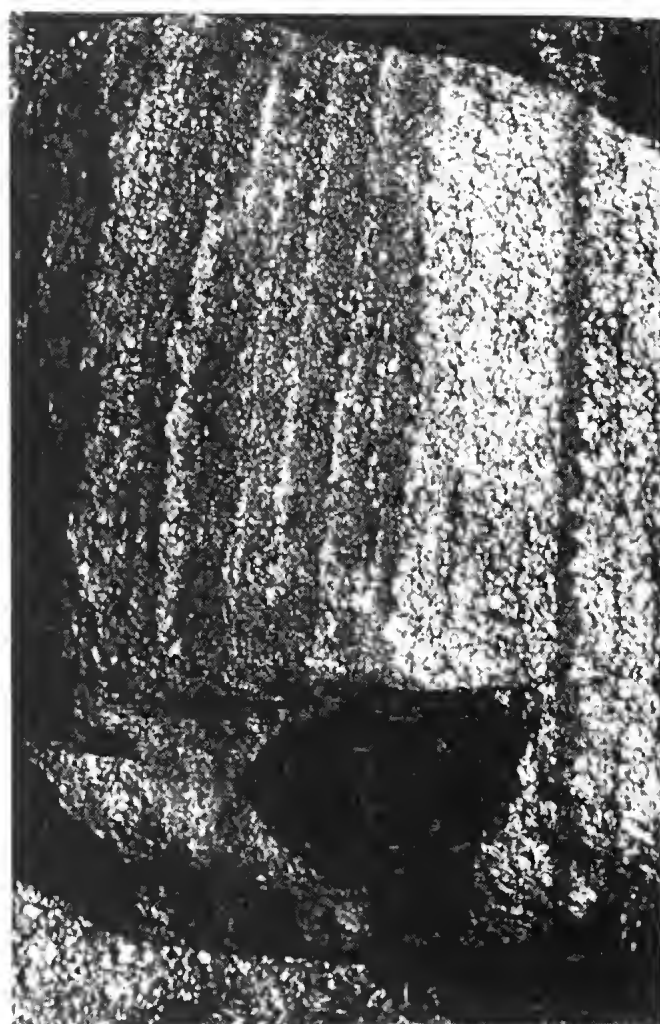
Figure 3 Alternating pyroxene-rich and feldspar-rich layers, Gilgarna Rock.

development of the microrhythmic layering. Similarly, lack of a relationship between layer spacing and crystal grain-size suggests that the processes of crystal nucleation, resorption and coarsening outlined by Boudreau (1987) are not significant at Gilgarna Rock. Notwithstanding the presence of minor disrupted blocks (Fig 4), the uniform and sharply defined layers at Gilgarna Rock are not consistent with the surge-type density currents and subsequent crystal mingling suggested as the major mechanism for under-saturated syenites of the Coldwell Complex, Ontario (Mitchell & Platt 1982).

The occurrence of these layering features within rocks derived from normally quite viscous magmas, leads to consideration of the processes capable of overcoming the limiting effects of high viscosity on the development of rhythmic layering. High viscosities in felsic melts result from a three-dimensional network of interconnected alumi-nate and silicate tetrahedra, where all oxygens form bridging bonds between pairs of tetrahedral cations (Dingwell & Myson 1985). The effects of fluxing compo-nents on such polymerized melts is to disrupt the network structure, depolymerize the melt, and thus enhance the diffusivity of components (Chorlton & Martin 1978; Picha-vant 1981; Manning 1981).

In a study of similar layering to that of Gilgarna Rock within the Calamity Peak granite of South Dakota, Rock-hold *et al.* (1987) concluded that the presence of fluxing components, such as boron or fluorine, can play a critical part in the development of rhythmic layering within granitic rocks. They suggested that depletion of boron in the melt, via tourmaline crystallization, decreased the solubility of H_2O in the melt, leading to the exsolution of an

aqueous fluid. This was responsible for shifts in phase equilibria, with alternating mineral products as the crystal-lization front moved through the melt leading to the development of rhythmic layering.

Tourmaline does not occur in the Gilgarna Rock syenite, however, a thorough geochemical investigation of a suite of Gilgarna Rock samples indicates fluorine levels as high as 1900 ppm (author's unpublished data). Emeleus (1963) stressed the importance of fluorine in promoting rhythmic layering in the Gardar granites of Greenland. Manning (1981) showed that fluorine can have a more pronounced influence than boron in driving the crystallizing magma towards Ab in the Qz-Ab-Or system, and in decreasing the solidus temperature.

At Gilgarna Rock, fluorine depletion in the melt, by incorporation into pyroxene and eventually fluorite, could have lead to the exsolution of an aqueous fluid during crystallization. Such an increase in fluid pressure is capable of decreasing liquidus temperatures to such an extent, that pyroxene replaces feldspar as the primary phase at the liquidus (Parsons & Becker 1987). In a closed system, regular mineral layering may occur via an internally self-regulating rhythmic process (eg Maaloe 1987), but at Gilgarna Rock, irregular layer thicknesses suggest an irregular control. Periodic and repetitive changes in vola-tile pressure, causing shifts in the position of the eutectic of the crystallizing system, and hence rhythmic alternation of mineral layers, were proposed by Redden (1963) for some layered rocks from South Dakota, and by Parsons and Becker (1987) for the Klokken complex of South Greenland. At Gilgarna Rock, a similar model is proposed, with irregular stages of pressure release resulting in periodic increases in liquidus temperatures, causing feldspar pre-cipitation. Subsequent build-up of fluid pressure due to further removal of fluorine from the melt could have returned the system to pyroxene precipitation, until the next stage of pressure release.

The confinement of the rhythmic layering to the margins of the coarse phase, and the stronger development of autometasomatic products in the medium phase adjacent to the contact zone, suggest that pressure release was facilitated via movement of the aqueous fluid into the medium phase in this zone. The sedimentary-type features, which indicate the localised presence of strong currents, display facing directions which are consistent with the progressive passage of fluids away from the interior of the coarse phase, towards the medium phase.

Figure 4 Scour and fill structures within coarse phase syenite, Gilgarna Rock. Arrow indicates facing direction; zone 1 represents early layering subsequently modified by scours 2 and 3. Note disrupted blocks in zone 1, syn-crystallization micro-faults within zones 2 and 3, and orbicular structure within late-stage relatively massive syenite, which truncates the base of zone 1.

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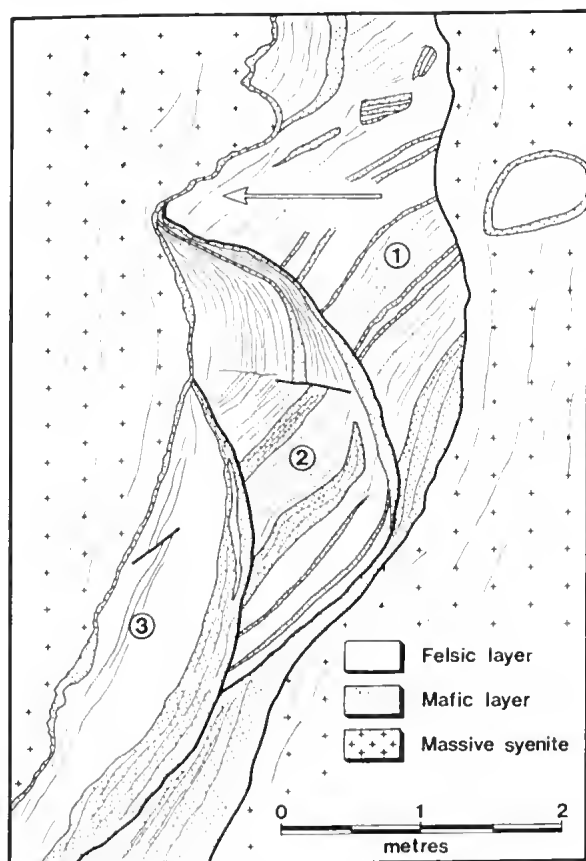
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Biomass of surface-foraging ants (Formicidae) in four bushland habitats in the wheatbelt of Western Australia

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Abstract

Using quadrat counts, biomass of surface-foraging ants was measured within four long unburnt bushland habitats in the Western Australian wheatbelt between January and November 1988. Bushland habitats were classified as mallee, woodland, shrubland and heath. Characteristics of plant litter, canopy and vertical density of vegetation to 3 m were determined for habitats. Prior to monthly ant counts, soil moisture and soil temperature were measured at 10 cm depths. Habitats differed significantly in biomass of surface-foraging ants. Mean dry ant biomass (+ S.E.) for mallee, woodland, shrubland and heath was 19.6 + 4.0, 6.9 + 1.1, 4.3 + 0.9 and 3.4 + 0.4 mg/m^2 respectively. Ants < 2 mm, 4 - 7 mm, and > 10 mm in length contributed little to biomass, irrespective of habitat. Ants 2 - 4 mm in length were most abundant in all habitats, accounting for 91 % of biomass in mallee. Ants 7 - 10 mm were also important in woodland, shrubland and heath. Biomass also varied temporally, with marked winter minima and summer maxima, and correlated with soil temperature in habitats other than heath. Soil moisture had no apparent effect on ant biomass, irrespective of habitat. The differences between the four habitats (with respect to plant litter, canopy and vertical density of vegetation) were assessed for the six possible pairs of habitats. Woodland and mallee were most similar, with 7/14 variables showing significant differences. Shrubland/woodland and shrubland/heath were most dissimilar, with 12/14 variables showing differences. Correlation analysis indicated that ant biomass was positively associated with woody litter, broad-leaf litter and vegetation density at 2.5 - 3 m height, and negatively with grassy litter, vegetation density at 0 - 0.5 m height, and the coefficients of variation of litter and canopy cover. These associations probably reflect the importance of these aspects of the habitats in providing ants with diversity of food and shelter, and suitable microhabitats and microclimates. The ant fauna in these reserves may reflect past disturbances or management strategies such as fire exclusion for at least 45 years, livestock grazing and selective logging for charcoal production.

Introduction

Ants are a conspicuous component of Australian ecosystems, being especially abundant and diverse in semi-arid environments where in excess of 150 species have been found within an area of only 0.5 ha (Andersen 1983, 1984). Given their abundance and diversity, ants fulfil a major role in ecosystems through soil aeration and drainage, nutrient and seed redistribution, plant pollination, and general predator-prey interactions (Buckley 1982, Abensperg-Traun 1988, Lobry de Bruyn & Conacher 1990).

Australian studies on ant ecology have examined their diversity (Andersen 1983, 1986), periodicity in patterns of activity (Briese & Macauley 1980, Andersen 1983), community structure (Briese & Macauley 1977, Morton & Davidson 1988), interactions with physical soil parameters such as structure and particle size distributions (Greenslade & Thompson 1981, Lobry de Bruyn 1990), their role in seed dispersal (Berg 1975, Drake 1981), short-term effects of fire on ant community parameters (O'Dowd & Gill 1984, Andersen & Yen 1985), and their usefulness as bioindicators (Majer 1983, Andersen 1990). Alternatively, they have focused on prominent species such as the meat ant *Iridomyrmex purpureus* (Greaves & Hughes 1974, Greenslade 1975, 1976) and bull ants, *Myrmecia* spp. (Gray 1971). Characteristics of vegetation, such as structural complexity, and plant litter, are known to influence ant populations in Australia (Greenslade and Thompson 1981, Andersen 1986). Few studies, however, have quantified the relationship between ant abundance and vegetation and plant

litter parameters (e.g. Majer *et al.* 1984). Sound knowledge of the conditions best suited for a thriving ant fauna is essential for the successful rehabilitation of degraded environments (Majer *et al.* 1984).

The Western Australian wheatbelt has experienced extensive land-clearing for agriculture between 1900 and 1970. Today, native vegetation remnants of the region are generally small, isolated to varying degrees and often degraded through livestock grazing and weed invasion. In addition, this study area has been unaffected by fire for at least 45 years, and this may have had a significant influence on its ant fauna (see O'Dowd & Gill 1984, Andersen & Yen 1985). Although an absence of fire since about 1945 is not unusual in the wheatbelt, other regions of Western Australia, such as the extreme southwest, have had more frequent fires. In recognition of the need to understand the ecological dynamics of these remnants, long-term research into its faunal and floral components is being conducted (Main 1987, Saunders *et al.* 1987). The present study forms a part of this research activity and was carried out as part of a larger study into the foraging ecology of the echidna (Abensperg-Traun 1990). It describes the results of an 11-month ant survey of four long unburnt habitats in two Western Australian wheatbelt reserves, and it emphazises surface-foraging ant species because these make up the bulk of ants in southern Australia (Greenslade 1979). The study has three aims: (i) to determine differences in biomass of surface-foraging ants in relation to habitat; (ii) to examine soil moisture and temperature as determinants of surface-activity; and (iii) to determine any associations that exist between vegetation and plant litter and biomass of surface-foraging ants.

Materials and Methods

Study area

The study was conducted in Durokoppin East Nature Reserve (31°24'S, 117°45'E; 1030 ha) and Kodj Kodjin Nature Reserve (31°27'S, 117°47'E; 204 ha) of the Western Australian wheatbelt, between January and November 1988. The Reserves lie <400 m above sea level with an altitudinal relief of <75 m. They are connected by a continuous strip of native vegetation 2.7 km long and 40 m wide. The region is semi-arid (Gentilli 1965), with a mean annual precipitation of 334 mm, which falls mostly in the winter months from May to August (Beard 1980). Ambient temperature and rainfall data for Kellerberrin are given in Table 1.

Table 1

Mean monthly rainfall (mm) and minimum and maximum monthly ambient temperatures (°C) for Kellerberrin (Beard 1980).

	J	F	M	A	M	J	J	A	S	O	N	D
Rainfall (mm)	10	15	22	22	43	57	53	42	26	18	11	13
Min. temp. (°C)	16	20	16	11	7	8	7	7	7	9	14	14
Max. temp. (°C)	34	34	32	25	22	20	17	17	22	24	29	29

The vegetation in these two reserves has been unburnt for at least 45 years. I grouped the vegetation into structural units (Beadle & Costin 1952) because we know these to be important influences on the abundance and distribution of the Australian ant fauna (Greenslade & Thompson 1981). Groups that I recognized were open woodland, mallee, shrubland and heath. Woodland, mallee and heath are fully described in Abensperg-Traun and De Boer (1990). Shrubland is dominated by *Allocasuarina campestris,* with some *Leptospermum* and *Melaleuca* species. It is dense (90-100% projected canopy cover), and grows to about 3 m in height. Ground cover is moderately extensive (40-50%) and consists of fallen debris from shrubby plants (mostly *Allocasuarina* needles), with some grasses and herbs. Surface lateritic gravel overlies sandy subsoils in most areas. The distribution and area of each habitat within the Reserves is given in Fig 1 and Table 2.

Table 2

Habitat contributions to reserve area

Habitats	Durokoppin Reserve		Kodj Kodjin Reserve	
	Area (ha)	% of reserve	Area (ha)	% of reserve
Woodland	321	31	112	55
Mallee	44	4	56	28
Shrubland	351	34	31	15
Heath	323	31	4	2
Other[1]	1	<1	1	<1

[1]rocky outcrops; gravel and sand pits.

For sampling purposes, I considered the two reserves as representing a single area of native vegetation because of their close proximity and connectivity to each other, because of the similarity of their soils, flora and fauna, and their similar fire history (Dell 1978, Muir 1978, Chapman & Kitchener 1978, Dell & Chapman 1978, W.M. McArthur, unpubl. manuscript). I distributed study plots unevenly between the reserves (Fig 1) because of difficulties to gain access to suitable patches of mallee in Durokoppin, and heath and shrubland in Kodj Kodjin.

Ant sampling

Pitfall traps are an accepted method to measure the activity of surface foraging ant species. Such traps integrate the whole 24-hour cycle of activity, as well as day-to-day variation, and are frequently used to assess Australian ant faunas (Greenslade 1973, Rossbach & Majer 1983). Yet during a previous study where pitfall traps were used (Abensperg-Traun 1988), a source of bias was identified. Here, individuals of a particularly abundant, small species of *Iridomyrmex* appeared to follow colony members into trapping pits, thus leading to potential overestimation of densities. For the present study, I therefore chose a visual sampling technique to measure spatial and temporal variations in biomass of surface-foraging species (Briese & Macauley 1980).

Ant densities in habitats were determined by counting ants in 10 randomly positioned 1 m^2 quadrats. These counts were carried out in each of six 2500 m^2 study plots for each habitat. Quadrat positions changed monthly. Shrubland was not sampled in January and February, and only two study plots were allocated to shrubland (see Table 3). Plots were sampled monthly, in random order, and at a time of day when ants were known from observation to be active, ie. early mornings during summer (at sunrise), and afternoons in winter (no sampling was done during rain). Given that relative, not absolute, abundances were measured, the fact that only a proportion of colony members are likely to have been active at any one time (Chew 1960) is not critical. To avoid pseudoreplication, plots were chosen such that they were in interspersed
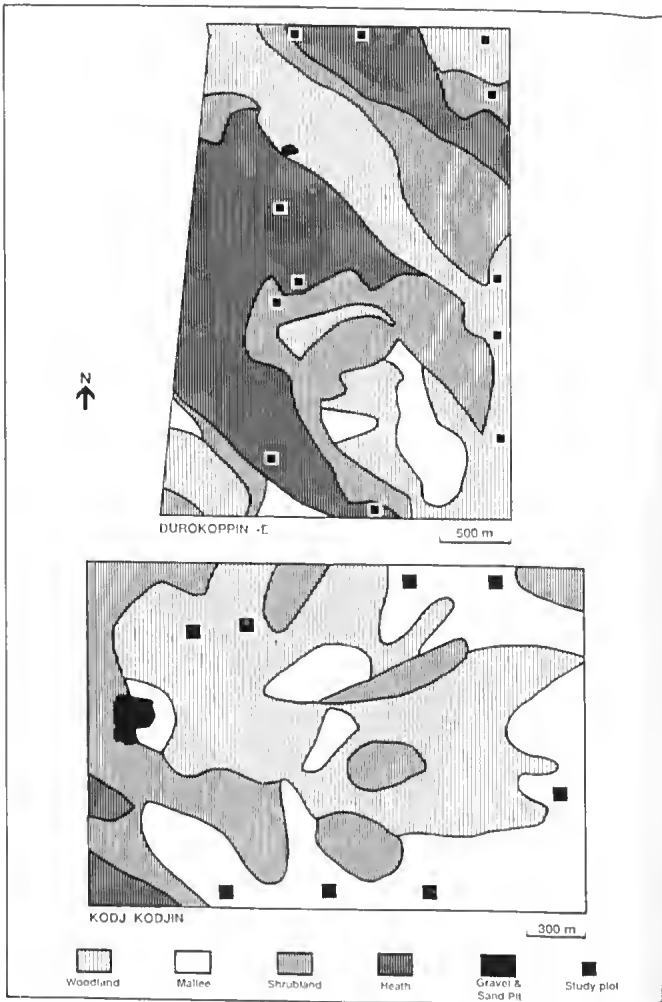

Figure 1. The distribution of study plots within the major vegetation types in Durokoppin and Kodj Kodjin Nature Reserves, Western Australia.

patches of the different habitats (Hurlbert 1984; Fig 1); the total area within which study plots were placed is given in Table 2. Surface foraging ants were counted and placed into five size categories: < 2 mm, 2 - 4 mm, 4 - 7 mm, 7 - 10 mm, and > 10 mm. Counts per quadrat lasted two minutes (see Anderson 1991). Dry mass was estimated from a linear regression between length and dry weight of ten local ant species representing the range of sizes and major castes, if dimorphic castes ($y = 0.366x + 0.024$; $r_0 = +0.94$, $P < 0.0001$; from Abensperg-Traun 1990).

The use of a quadrat method to measure ant activity and the restriction of sampling to daytime periods may have introduced two potential sources of bias: (i) the differential sampling of diurnal vs. nocturnal species (see Briese & Macauley 1980, Andersen 1983). While strictly nocturnal species probably were not sampled, most surface-foraging species were accounted for because I sampled very early mornings in summer and afternoons in winter when ants are believed to be most active in southern Australia (Andersen 1983). By comparing habitats based on ant biomass on the surface (at sampling time), I assume that the contribution of nocturnal species to surface biomass is similar for the range of habitats that I measured. This is a reasonable assumption because opportunistic examinations at night suggested that the activity of the most abundant species (*Iridomyrmex*) extended well into the sampling period, and only a small number of species provide the bulk of ants in the study area. In fact, numerically, Abensperg-Traun (1988) found a single, small species of *Iridomyrmex* to account for the majority of ants sampled in all the habitats. Nevertheless, biomass values may be underestimates; and (ii) the potential over-sampling of large vs. small ants. Counting ants in quadrats may result in a bias in favour of larger ants because small ants are difficult to see, especially in areas of abundant litter. I took great care to locate such specimens by turning over plant litter.

Soil variables

In southern Australia, soil temperature and soil moisture are the predominant influences on the foraging activity of ants (Andersen 1986). My observations suggested that the nests of the numerically dominant *Iridomyrmex* lie close to the soil surface, hence I measured these two parameters at 10 cm depth in all the habitats except shrubland, taking one measure from each study plot and for every month. Soil temperature was determined by using copper-constantan welded tip P.T.F.E. insulated (type K) thermocouples (Taylor & Jackson 1965, Haverty *et al.* 1975). The soldered temperature-sensitive junctions were buried at 10 cm depth for the duration of the study. The positive and negative ends were plugged and protectively stored in a buried styrofoam container just below the soil surface which allowed instant temperature readings to be taken through a digital hand-held temperature indicator, and without disturbing ant activity. Details of soil moisture measurement were given in Abensperg-Traun and De Boer (1990). Both soil moisture and temperature were determined five minutes prior to ant counts.

Table 3

Experimental design and ant sampling regime.

Habitats Sampled for ants	Number of study plots		No. of months sampled	No. of monthly ant quadrats per plot	Tot. no. of ant quadrats per plot
	Durokoppin Reserve	Kodji Kodjin Reserve			
Woodland	4	2	11	10	660
Mallee	0	6	11	10	660
Shrubland	2	0	9	10	180
Heath	6	0	11	10	660

Vegetation variables

I measured 14 variables at 36 predetermined sampling stations in each study plot (at regular 10 m intervals) once: (i) the percentage of soil surface covered by plant litter in a 1 m^2 quadrat, LITT; (ii) the coefficient of variation of litter cover, CVLITTCOV, calculated from "(i)"; (iii) the amount of woody litter, calculated as a percentage of "(i)" (twigs, branches, logs, *Eucalyptus* nuts, bark), WOODYLITT; (iv) the amount of broad-leaf litter, calculated as a percentage of "(i)" (*Eucalyptus* spp.), BROADLITT; (v) the amount of narrow-leaf litter, calculated as a percentage of "(i)" (*Allocasuarina* spp. and assorted shrubs), NARRLITT; (vi) the amount of grassy litter, calculated as a percentage of "(i)" (including herbs and sedge, such as *Ecdeiocolea monostachya*), GRASSLITT; (vii) the percentage of pro-jected canopy cover, measured from ground level using a spherical densiometer as in Lemmon (1956), CANCOV; (viii) the coefficient of variation of canopy cover, CVCAN-COV, calculated from "(vii)"; (ix) the vertical density of vegetation at a height of 0 - 0.5 m, VEG 0 - 0.5 m; (x) at 0.5 - 1 m, VEG 0.5 - 1 m; (xi) at 1-1.5 m, VEG 1 - 1.5 m; (xii) at 1.5 - 2 m, VEG 1.5 - 2 m; (xiii) at 2 - 2.5 m, VEG 2 - 2.5 m; and (xiv) at 2.5 - 3 m, VEG 2.5 - 3 m. Vegetation density was measured with a canopy intercept method where a rod is passed vertically through the vegetation and the number of vegetation intercepts within the specified strata are counted. An increase in the number of intercepts is interpreted as an increase in vegetation density (Frank and McNaughton 1990).

Analysis

The following transformations were made to improve linearity of the data: mean ant biomass (log); vegetation density (square root); percentage litter cover, litter type and canopy cover (arcsine) (Underwood 1981). To deter-mine the effects of habitats and time on ant biomass, I analysed means of quadrats of ant biomass within the plots (dry weight mg/m^2) by non-orthogonal split-plot ANOVA (Steel & Torrie 1981). Using the the mean values for study sites, I applied simple linear regressions to correlate ant biomass with soil, litter and vegetation variables. Habitat differences in plot means of plant litter and vegetation values were analysed by Tuckey's Paired Comparison Procedure (Tuckey 1953). Computations were carried out using GENSTAT 5 Release 1.3 (Sun/Unix) (Payne *et al.* 1988).

Results

Ant biomass and soil variables

Ant biomass generally followed an annual cycle, with peaks and troughs at hottest and coldest times of the year, respectively. These fluctuations were most pronounced in mallee and least pronounced in heath (Fig 2). Surface ant biomass was independent of soil moisture at 10 cm depth, regardless of habitat, but was significantly correlated with soil temperature at 10 cm depth in woodland ($r = +0.87$, d.f. = 10, $P < 0.001$) and mallee habitats ($r = +0.92$, d.f. = 10, $P < 0.001$). In heath, biomass remained relatively constant throughout the year, suggesting that ants may have foraged evenly between seasons. Soil temperature at 10 cm depth was thus not a good predictor of ant activity in heath. Woodland, mallee and shrubland biomass declined sharply when soil temperature near the surface fell below about 17° C. Monthly soil temperature and soil moisture did not vary significantly between the habitats ($P > 0.05$).

Ant biomass and vegetation variables

There was a highly significant effect of habitat on ant biomass (Table 4). This strong habitat effect was estimated from the between-habitat variance of ant biomass of 35.7689 on 3 degrees of freedom, as against a within-habitat

estimate of variance of 3.1995 on 11 degrees of freedom. Orthogonal comparisons indicate that most of this strong habitat effect was accounted for by differences between mallee and the remaining habitats (F = 27.64, d.f. = 1/11, P < 0.001). There was a significant effect of time (month) on biomass, and a significant habitat x time (month) interaction (Table 4). The interaction was probably due to the large increase in ant biomass in the mallee habitat from November to March, which exceeded the increase in all other habitats (Fig 2).

The mean number of ants/m² (± S.E.) in each habitat was 18.0 ± 3.6 (mallee), 5.2 ± 1.0 (woodland), 2.7 ± 0.8 (shrubland) and 2.0 ± 0.3 (heath) (Table 5). Mallee had the highest biomass in all months except July, when ant activity was lowest and habitats were most similar. Mean ant biomass (dry mg/m²) in each habitat was 19.6 ± 4.0 (mallee), 6.9 ± 1.1 (woodland), 4.3 ± 0.9 (shrubland) and 3.4 ± 0.4 (heath). The ant size categories of 2 - 4 and 7 - 10 mm were most abundant in woodland, heath and shrubland habitats, while in mallee only ants of 2 - 4 mm length were abundant, accounting for 91% of biomass (Table 6). Most specimens in the 2 - 4 mm category were attributed to a single species of *Iridomyrmex*. Ant size categories other than those between 2 - 4 and 7 - 10 mm contributed little to total biomass in all habitats.

Characteristics of litter and vegetation are given in Tables 7 and 8 and Fig 3. Woodland and mallee were most similar, with 7/14 variables showing significant differences. Shrubland/woodland and shrubland/heath were most dissimilar, with 12/14 variables showing differences.

Ant biomass (averaged across all monthly samples) was positively correlated with woody litter, broad-leaf litter and vegetation density at 2.5 - 3 m, and negatively with grassy litter, vegetation density at 0 - 0.5 m and the coefficients of litter cover and canopy cover, but not with other variables (Fig 4). However, r^2 values were low, accounting for < 54 % of the variation in ant biomass.
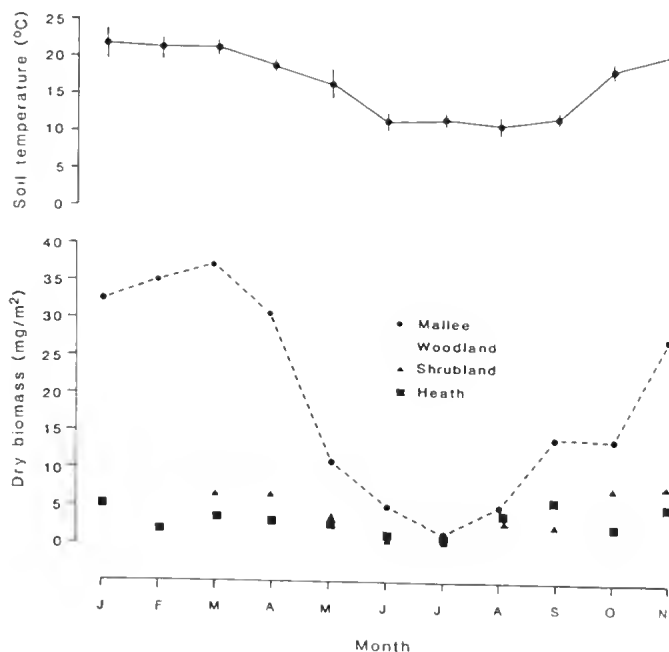
Figure 2. The relationship between soil temperature (°C) at 10 cm depth (mean across all habitats, + S.E.), and monthly fluctuations of dry ant biomass (mg/m²) on the soil surface for woodland, mallee, shrubland and heath habitats. Average standard errors of the mean ant biomass: woodland 3.6, mallee 13.3, shrubland 2.8, heath 1.5 mg/m². Mallee data points have been joined so as to highlight the observed differences in ant biomass between mallee and the other habitats.

Discussion

Ant biomass and soil variables

Observed activity patterns showing summer maxima and winter minima are characteristic of ant faunas subjected to marked seasonal climatic regimes (Majer 1980, Greenslade & Greenslade 1984). While foraging activities in ants may also be influenced by biotic factors such as the presence and condition of larvae in nests, food availability and amounts of food stored (Weber 1972, Whitford & Ettershank 1975), surface activity in this study was strongly

Table 4

Summary table of non-orthogonal analysis of variance (via regression) of dry ant biomass (mg/m²).

Source of variance	d.f.	s.s.	m.s.	F	P
Study plots	5	7.8025	1.5605	<1	n.s.
Habitats	3	107.3067	35.7689	11.18	**
Error	11	35.1946	3.1995		
Months	10	108.2027	10.8203	13.37	***
Habitats x months	28	36.3691	1.2989	1.60	*
Error	158	127.8900	0.8094		
Total	215	422.7656	1.9664		

* 0.01 < P < 0.05
** 0.001 < P < 0.01
*** P < 0.001
n.s. not significant

Table 5

Mean number of ants per m² (± S.E.) for each month in woodland, mallee, shrubland and heath habitats.

Month	Habitat			
	Woodland (n¹ = 60)	Mallee (n = 60)	Shrubland (n = 20)	Heath (n = 60)
January	12.1±1.7	30.0±1.3	N.S.²	4.3±0.9
February	8.2±1.8	31.3±2.0	N.S.	1.9±0.2
March	7.4±1.3	34.0±0.9	3.3±0.4	1.3±0.2
April	6.4±0.9	26.7±1.1	5.2±0.3	1.9±0.1
May	6.1±0.9	10.4±0.9	1.8±0.1	1.7±0.2
June	1.5±0.3	4.3±0.7	0.5±0.1	1.0±0.2
July	1.8±0.2	1.9±0.1	0.3±0.1	0.5±0.2
August	1.8±0.4	4.4±0.8	0.2±0.1	1.3±0.2
September	3.3±0.2	15.3±0.5	1.6±0.3	2.5±0.5
October	2.8±0.3	12.7±0.8	5.7±0.1	1.5±0.1
November	5.7±0.9	27.5±1.0	5.8±1.6	3.7±0.6
December	N.S.			
Mean (all months)	5.2±1.0	18.0±3.6	2.7±0.8	2.0±0.3

¹n = monthly number of sample quadrats. ²N.S. = Not sampled.

Table 6

The percentage contribution of ant size categories (measured in mm) to total dry biomass on the soil surface for woodland, mallee, shrubland and heath habitats (mean ± S.E.).

Habitat	% Contribution of Ant Size Categories				
	<2	2-4	4-7	7-10	>10
Woodland	7.8±2.6	45.6±3.9	1.4±0.5	44.4±4.7	0.8±0.5
Mallee	5.1±1.5	91.2±1.7	0.1±0.1	3.5±1.4	0.1±0.1
Shrubland	1.1±0.7	56.9±6.7	0.0	41.6±6.4	0.4±0.2
Heath	1.0±1.3	40.9±3.3	1.2±0.6	55.7±3.3	1.2±0.6

associated with soil temperature in woodland and mallee faunas, though not in heath. The observed lack of an association between foraging activity in heath and soil temperature may have been due to insufficient foraging data (ie. low numbers of ants) rather than differences in ant tolerance to soil temperature extremes. While soil moisture apparently did not directly affect biomass, humidity did influence ant activity as evidenced by incidental observations showing increases in nest excavations when levels of humidity were high, such as shortly before and after rain.

Ant biomass and vegetation variables

Characteristics of vegetation influence ant communities through their effects on microclimate, carrying capacity (food sources and quantities) and structural complexity of the habitat (Greenslade & Greenslade 1977). Biomass of surface-foraging ants was high where woody litter, broad-leaf litter and vegetation density at 2.5 - 3 m were also high. These variables probably represent factors which contribute to habitat complexity which, elsewhere, are known determinants of the abundance of ants (Greenslade & Thompson 1981, Greenslade & Halliday 1983). Woody and broad-leaf litter provide nesting and foraging sites, microhabitats, food supplies and shelter from ambient temperature extremes (Greenslade & Greenslade 1977), while small trees (2.5 - 3 m) might provide food such as seeds, insects and sap (Andersen 1983), and protection from heat and direct sunlight, and possibly also higher relative humidity due to shade.

Biomass was low where grassy litter, vegetation density at 0 - 0.5 m, and the coefficients of variation of litter and canopy cover were high. Ants thus favoured areas of evenly distributed litter and canopy. The importance of an even canopy cover might reflect the need for suitable microclimatic conditions (shade) for foraging, which is probably of particular significance in the Western Australian wheatbelt where summer air temperatures reach 45°C in the shade. I have observed that dense vegetation at ground level is often associated with lack of bare patches of soil, and such areas are often avoided by foraging ants (Andersen 1983). Greenslade and Thompson (1981) also found certain species to be absent under dense vegetation, which they attributed to the relatively low temperatures experienced under such conditions. High values of grassy litter were generally associated with *Ecdeiocolea monostachya* (sedge) in heath, which was not favoured by ants. Sedge litter appears comparatively unsuitable for providing ants with diversity of microhabitat and adequate sources of food.
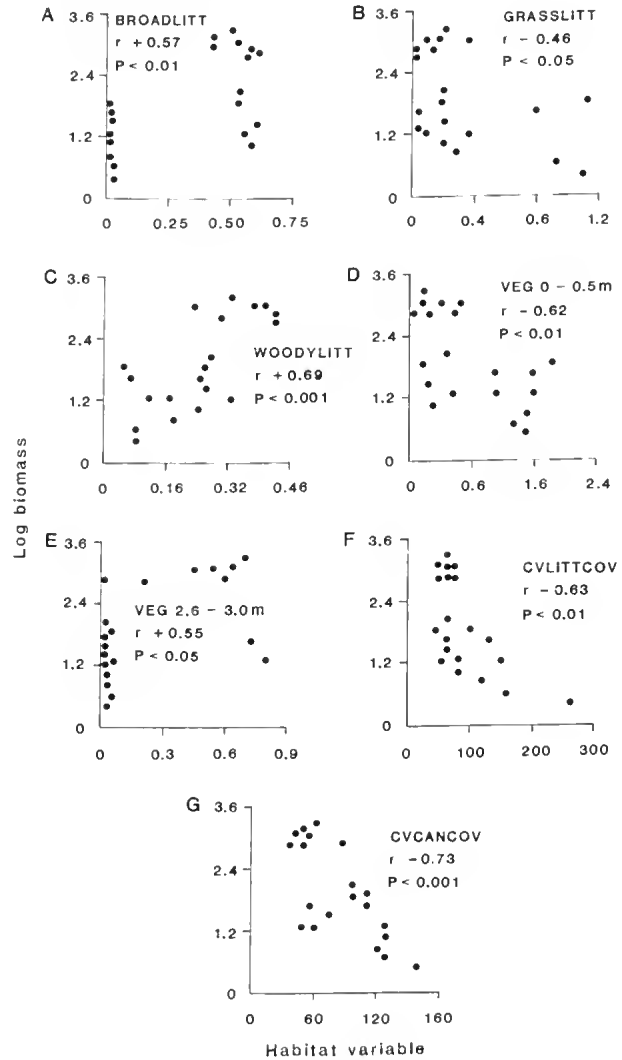
Figure 4. Correlations between log ant biomass (average of all months) and seven plant litter and vegetation variables for twenty study plots in four vegetation structural units (df = 18). Only those variables with significant correlations are listed. A broad-leaf litter (BROADLITT); B grassy litter (GRASSLITT); C woody litter (WOODYLITT); D vegetation density at 0 - 0.5 m height (VEG 0 -0.5 m); E vegetation density at 2.5 - 3.0 m height (VEG 2.5 - 3.0 m); F coefficient of variation of litter cover (CVLITTCOV); G coefficient of variation of canopy cover (CVCANCOV).
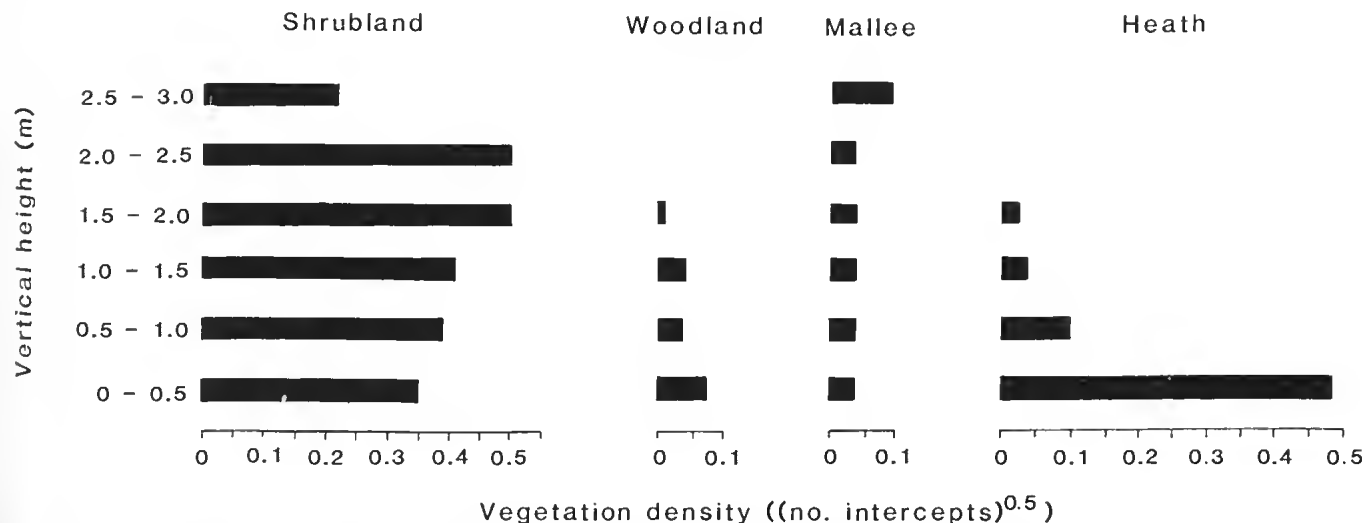
Figure 3. Vertical vegetation density [(number of intercepts)$^{0.5}$] between 0 and 3 m for the four habitats.

Greenslade (1979, p 3) stated that (in the South Australian environment) "the ideal situation for ants consists of a mosaic of bare soil and areas of herbs, small shrubs and grasses, under an open canopy of trees or taller shrubs". Andersen (1983) considers mallee vegetation to closely resemble Greenslade's (1979) ideal habitat for ants. In the Western Australian wheatbelt, mallee is apparently also the most suitable habitat for ants because biomass was highest there. Despite the similarity of woodland and mallee habitats in many of the habitat parameters measured (Table 8), there are potential explanations for the enormous biomass difference between these two habitats. Mallee is characterized by relatively large areas of bare ground, interspersed with areas of abundant litter, and these are often favoured for unimpeded foraging and nest excavation in ants (Andersen 1983). Further, more abundant broad-leaf litter and a higher vegetation density at 2 -3 m height in mallee may provide more abundant and diverse sources of food and a favourable microhabitat and microclimate.

Ant biomass for woodland was significantly higher than that for heath (t = 2.91, d.f. = 65, P < 0.005). In an eastern Australian study, Andersen (1986) also found ants to be more abundant in woodland, and he attributed this difference to woodlands' greater structural complexity; one would expect ant faunas at Kellerberrin to be similarly affected. Low ant biomass in heath may be due to the lack of intermediate-sized shrubs and trees, low diversity of plant litter and soils that are very sandy (and thus possibly not sufficiently stable for subterranean nest and gallery construction for some ant species). Shrubland had low ant biomass, possibly because canopy frequently approached 100% cover and afforded little light at ground level, thus adversely affecting microclimatic conditions (Carlson &

Gentry 1973, Greenslade & Thompson 1981). The diversity of litter as a source of food was low, with only a small woody and broad-leaf component. Shrubland is relatively poor in seed production (Van Schagen 1986), and seeds may form important dietary items for harvesting species such as *Pheidole* and *Monomorium* (Briese 1974); termite abundance in shrubland is also comparatively low (Abensperg-Traun & De Boer 1990), and I have observed termites to be important food for predatory *Iridomyrmex* (also reported in Greenslade 1970).

The observed weak associations ($r^2 < 54\%$) between ant biomass and vegetation and litter characteristics may have been influenced by a range of factors inherent in the study design. For instance, only extremes of habitat were sampled, thus a few points in one particular habitat may have had a strong influence on the strength of the association (e.g. see Fig 4A). Further effects may derive from the use of 11-month averages for ant biomass data, the measurement of physical habitat characteristics (vegetation structure and plant litter) at only one time and in different quadrats to the biomass measurements, and the uneven distribution of study plots between the two reserves. However, given the similarity of soil, vegetation and fire history of these closely adjacent reserves, it is unlikely that their ant faunas differ significantly in abundance and composition.

The Nature Reserves at Kellerberrin have experienced a range of disturbance regimes in the past. Woodland and mallee, in particular, were subjected to selective logging for charcoal production (between 1940 and 1945) as well as periodic livestock grazing, thereby reducing its naturally sparse understorey and possibly also affecting soil structure through hoof-pressure (King & Hutchinson 1976). Intermittent livestock grazing continues along the reserve margins during sheep mustering. Such disturbance re-

Table 7

Habitat characteristics of plant litter and canopy (mean ± S.E.).

Habitat	n[1]	Litter Cover (%)	Litter type (%)				Canopy Cover (%)	CV[2] Litter Cover	CV Canopy Cover
			Woody	Broad-leaf	Narrow-leaf	Grasses + herbs			
Woodland	216	51±3	46±2	37±2	6±1	11±2	34±3	59±5	71±11
Mallee	216	35±5	36±2	53±4	3±1	8±3	39±1	62±5	51±3
Heath	216	9±1	10±6	1±1	24±21	65±27	14±1	155±23	124±8
Shrubland	72	46±2	14±2	2±1	79±3	5±1	91±4	71±4	50±1

[1]n = sample size
[2]CV = coefficients of variation

Table 8

Summary table of Studentized Range Values[1] of comparisons between pairs of habitats for plant litter and vegetation parameters, using Tuckey's Paired Comparison Procedure (Tuckey 1953).

Variables	W v M[2]	W v H	W v S	M v H	M v S	H v S
% Litter cover	12.81**	58.16**	7.72**	35.97**	10.23**	35.67**
Litter variability (CV)	0.251	7.27**	0.59	4.05*	0.41	35.67**
% Canopy cover	1.28	6.98**	11.66**	6.21**	18.38**	6.44**
Canopy variability (CV)	5.41**	5.33**	3.86*	10.74**	0.04	27.17**
% Woody litter	3.60*	4.83*	3.76*	6.03**	7.36**	6.24**
% Broad-leaf litter	3.53*	32.37**	18.84**	28.85**	20.58**	2.18
% Narrow-leaf litter	0.10	3.03*	8.48**	3.10	14.79**	0.18
% Grassy litter	0.27	6.10**	1.02	7.27**	0.83	10.40**
Veg. density 0-0.5 m	0.47	19.07**	8.89**	11.39**	6.76**	4.87*
Veg. density 0.5-1 m	1.10	1.21	11.78**	1.99	21.50**	10.18**
Veg. density 1-1.5 m	0.04	0.23	33.75**	0.25	58.49**	18.69**
Veg. density 1.5-2 m	3.76*	1.18	56.99**	3.65*	93.39**	58.13**
Veg. density 2-2.5 m	5.32**	0.49	62.69**	6.83**	101.06**	97.04**
Veg. density 2.5-3 m	5.84**	—	8.83**	8.26**	7.04**	107.90**

[1]Levels of significance are indicated by * 0.01 < P < 0.05, ** P <0.01; — insufficient data.
[2]W = woodland, M = mallee, H = heath, S = shrubland.

gimes might favour ant species that thrive in disturbed environments (e.g. *Iridomyrmex*). The overwhelming numerical dominance and surface biomass of a single species of *Iridomyrmex* (c. 3 mm) in mallee, and to a lesser extent in woodland (see also Abensperg-Traun 1988), might be indicative of an opportunistic species exploiting a disturbed environment. This study provides no data on numbers of species for habitats. Yet, recalling the 71 species recorded from two 50 m x 25 m plots in semi-arid mallee of north-western Victoria (Andersen 1983), observations in this study suggest that the mallee ant fauna at Kellerberrin was of comparatively low species diversity.

It needs to be understood that the habitats that I measured have been unaffected by fire for at least 45 years. Yet fire is an important factor in the regeneration of *Eucalyptus* spp. through seed fall and the activities of harvester ants (Ashton 1979, O'Dowd & Gill 1984). Also, fire is known to increase seed-predator satiation (Wellington & Noble 1985, Andersen 1988), thus increasing the success of seedling establishment (Andersen and Yen 1985). I observed a general absence of young eucalypts in woodland and mallee, and this may well be a consequence of an altered fire regime (R Hobbs, personal communication).

Similarly, ant faunas may benefit by periodic fire through a release from competition with increasingly dominant species, such as *Iridomyrmex* (Greenslade 1976, Whelan 1980, O'Dowd & Gill 1984, Andersen & Yen 1985). The overwhelming numerical dominance of a single species of *Iridomyrmex* in mallee and woodland habitats may well be sustained and exacerbated by the prolonged exclusion of fire as a factor of disturbance. The associated consequences to the maintenance of ecological processes, such as seedling survival through seed dispersal by ants, are poorly understood. Given the long duration of fire exclusion in Durokoppin and Kodj Kodjin Nature Reserves, the present study could be used as the basis for experimental studies into fire-ant-habitat interactions.

In summary, of the four habitats that I measured, biomass of surface-foraging ants was overwhelmingly superior in mallee, possibly because the combination of abundant woody- and broad-leaf litter, and high vegetation density at a height of 2.5 - 3 m, provided ants with diverse and abundant food and shelter, microhabitats and suitable microclimates. In the Western Australian wheatbelt, mallee may therefore most closely resemble Greenslade's "ideal" habitat for ants. However, the bushland reserves that formed the basis of this study have been unaffected by fire for at least 45 years. This, combined with past disturbances such as logging and grazing, may have influenced the relative suitability of woodland, mallee, shrubland and heath for foraging ants.

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Recent Advances in Science in Western Australia

Earth Sciences

The Devonian carbonate rocks in the Geikie Gorge region have undergone a long and complex diagenetic history. Almost all primary porosity was destroyed by burial diagenesis in the Devonian-Early Carboniferous, accompanied by dolomitisation and secondary porosity development. Subaerial exposure during the Late Carboniferous and burial during the Permian-Cenozoic periods influenced karstification and calcite cementation, according to M W Wallace and associates working with the Geological Survey of WA:

Wallace M W, Kerans C, Playford P E, & McManus A 1991 Burial diagenesis in the Upper Devonian reef complexes of the Geikie Gorge region, Canning Basin, Western Australia. Bulletin of the American Association of Petroleum Geologists 75:1018-1038.

A J Mory of the WA Geological Survey recognizes seven phases in the evolution of the offshore Bonaparte Basin, northwestern Australia: Cambrian-Ordivician interior sag, Silurian-Early Devonian trough infill, Late Devonian-Carboniferous northwest-trending rifting, Permian-Carboniferous interior sag, latest Permian-Jurassic trough infill, Late Jurassic-earliest Cretaceous northeast-trending rifting and continental breakup, and Cretaceous and Cainozoic trailing-edge marginal sag:

Mory A J 1991 Geology of the offshore Bonaparte Basin northwestern Australia. Western Australia Geological Survey, Report 29.

Plio-Pleistocene events in the coastal deposits of the Carnarvon and Perth Basins are recorded by G W Kendrick and associates of the WA Museum and the University of WA. In the Perth Basin deposition of Pliocene to Early Pleistocene siliciclastic sediments in shoreline, inner shelf and regressive dune facies ended with a major regression and significant faunal extinction. Bioclastic carbonates characterise the Middle and Late Pleistocene in both basins and contain evidence of sub-tropical events including a southerly expansion of warm-water corals, suggesting a strengthening of the Leeuwin Current:

Kendrick G W, Wyrwoll K H, & Szabo B J 1991 Pliocene-Pleistocene coastal events and history along the western margin of Australia. Quaternary Science Reviews 10:419-439.

The Ashburton Basin is an arcuate belt of Proterozoic low-grade meta-sedimentary and meta-volcanic rocks flanking the southern and western margins of the Pilbara Craton, report A M Thorne and D B Seymour of the WA Geological Survey. Following continental rifting and breakup of the Pilbara Craton about 2.8-2.7 Ga, a phase of sedimentation occurred, represented by the upper Fortescue, Hamersley, Turee Creek and lower Wyloo Groups. This was followed by continental crustal collision between 2.0-1.7 Ga (the Capricorn Orogeny) and subsequent deformation and sedimentation 1.7-1.5 Ga:

Thorne A M & Seymour D B 1991 Geology of the Ashburton Basin Western Australia. Western Australia Geological Survey, Bulletin 139.

Continuous sedimentation occurs across the boundary between Frasnian and Famennian reef platforms in the Canning Basin. M R House of the University of Southampton and colleagues in the Geological Survey of WA find no evidence for meteorite or bolide impact events at this boundary - the previously-reported iridium anomaly postdates the Frasnian/Famennian boundary and was formed by cyanobacterial concentration. Several sea level changes occur in the boundary beds. One regressional event may correspond to the latest Frasnian sea level regression as observed elsewhere in the world:

Becker R T, House M R, Kirchgasser W T, & Playford P E 1991 Sedimentary and faunal changes across the Frasnian/Famennian boundary in the Canning Basin of Western Australia. Historical Biology 5:183-196.

Life Sciences

Parrots are not only a spectacular part of the fauna of arid Australia, but also have among the lowest reported water economies (ratio of evaporative water loss to metabolic rate) reported for desert-adapted birds. J B Williams of the University of Cape Town, South Africa, and co-authors from the University of WA found that a variety of species of parrots maintain a high metabolic rate whilst conserving water. This contrasts with other desert birds which have low metabolic rates to reduce water loss and conserve energy:

Williams J B, Withers P C, Bradshaw S D & Nagy K A 1991 Metabolism and water flux of captive and free-living Australian parrots. Australian Journal of Zoology 39:131-142.

The Diamond Dove is well adapted physiologically to life in arid and semi-arid mulga regions of central and western Australia. Despite its small size (the second smallest dove on record), it tolerates high body temperatures and relies on gular flutter to evaporatively cool when heat-stressed, according to E Schleucher and R Prinzinger of the Johann Wolfgang Goethe-University, Germany, and P C Withers at the University of WA:

Schleucher E, Prinzinger R & Withers P C 1991 Life in extreme environments: investigations on the ecophysiology of a desert bird, the Australian Diamond Dove (Geopelia cuneata Latham). Oecologia 88:72-76.

The fungus (*Phomopsis leptostromiformis*) that causes lupinosis in sheep grazing lupin stubbles infects lupin plants throughout the growing season but normally does not grow and produce toxins in plant tissue until after the plants die. P M Williamson and colleagues (University of WA and WA Department of Agriculture) report that these latent infections in living plants are arrested between the epidermis and the cuticle with the production of a unique coralloid mycelium. These structures were absent or much reduced in size on a breeder's line with high field resistance to Phomopsis stem blight:

Williamson P M, Sivasithamparam K, & Cowling W A 1991 Formation of subcuticular coralloid hyphae by *Phomopsis leptostromiformis* upon latent infection of narrow-leafed lupins. Plant Disease 75:1023-1026.

Note from the Hon Editor: This column needs your contributions! "Recent Advances in Science in Western Australia" may include papers that have caught your attention or that you believe may interest other scientists in Western Australia and abroad. This column helps to link the various disciplines and inform others of the broad spectrum of achievments of WA scientists (or others writing about WA). It is not intended to be an elite list of major advances. Members or non-Members of the Royal Society of Western Australia are encouraged to submit short (2-3 sentence) summaries of recent papers by Western Australian scientists or others writing about Western Australia, together with a copy of the title, abstract and authors' names and addresses, to the Hon Editor or a member of the Publications Committee: Dr S D Hopper (Life Sciences), Dr A E Cockbain (Earth Sciences), and Assoc Prof J Webb (Physical Sciences). Final choice of articles is at the discretion of the Hon Editor.

"Letters to the Editor" are also published at the discretion of the Hon Editor. Please submit a word processing disk with letters and suggest potential reviewers or respondents to your letter. *W A Cowling, Hon Editor, Journal of the Royal Society of WA.*

Honorary Members, Honorary Associate Members and Medallists of the Royal Society of Western Australia

Honorary Members (18)

[*Rule 11d of the Constitution: The Society...may...admit as Honorary Members persons distinguished in Science or as patrons thereof,...the number of such members shall not exceed 25*]

Name			Date Admitted to Ordinary Membership	Date Admitted to Honorary Membership
Miss	A M	Baird	1928	1973
Dr	J S P	Beard	1962	1990
Mr	G H	Burvill	1929	1973
Mr	W H	Cleverly	1938	1982
Mr	S J	Curry	1966	1989
Dr	J J E	Glover	1956	1982
Prof	B J	Grieve	1948	1975
Mr	A B	Hatch	1958	1982
Dr	E P	Hodgkin	1946	1975
Mrs	C F H	Jenkins	1933	1965
Mr	C F H	Jenkins	1929	1973
Dr	L E	Koch	1958	1989
Prof	A R	Main	1951	1982
Dr	D	Merrilees	1959	1979
Prof	R T	Prider	1932	1976
Mr	G G	Smith	1951	1979
Prof	Curt	Teichert	1938	1975
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[*Rule 11e of the Constitution: The Society...may...admit as Honorary Associate Members persons interested in Science,...the number of such members shall not exceed 25*]

Name			Date Admitted to Ordinary Membership	Date Admitted to Honorary Associate Membership
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Dr	W F	Cole	1939	1989

Medallists (16)

[*Rule 62 of the Constitution: A medal shall be awarded...every fourth year...for distinguished work in science connected with Western Australia*]

Name			Year Awarded Medal
Dr	W J	Hancock	1924
Dr	E S	Simpson	1929
Mr	W M	Carne	1933
Mr	G	Maitland	1937
Prof	E de C	Clarke	1941
Mr	L	Glauert	1941
Mr	C A	Gardner	1949
Dr	H W	Bennetts	1955
Prof	E J	Underwood	1959
Mr	C F H	Jenkins	1966
Prof	R T	Prider	1970
Prof	R M	Berndt	1979
Em Prof	B J	Grieve	1979
Dr	D L	Serventy	1979
Dr	J S P	Beard	1983
Em Prof	C A	Parker	1986

Response of Tree Canopy Species of Kings Park, Perth, Western Australia to the Severe Summer Wildfire of January 1989

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Abstract

Plant communities subjected to severe and repeated perturbations tend to show simplified structure. Kings Park, an area originally reported to contain a eucalypt-sheoak (*Eucalyptus-Allocasuarina*) forest, has been sequentially reduced to a mixed woodland of sheoaks and banksia (*Banksia*), and more recently to a woodland dominated by sheoaks. Of the trees surveyed in the natural bushland section of Kings Park following the severe January 4, 1989 wildfire, only 37% were showing epicormic resprouts after 3 months. By September 1989 a total of 61% displayed either epicormic stem resprouts or basal resprouts and by May of 1990, following further resprouting, but also some later deaths, the total tree survival was 68% of the original tree population. Of this 68%, however, only 16% retained canopy resprouts after one year; the remainder essentially being reduced to the level of the shrub layer. At the level of species, the sheoak, *Allocasuarina fraseriana*, showed slightly better survival compared to the banksias, *B. attenuata*, *B. menziesii* and *B. grandis*, which, in turn, were better than any remnant eucalypts. Surviving trees tended to be trees of smaller than average diameter or height. Future summer fires are expected to further reduce the remaining tree canopy, thus further reducing the structural diversity of the native regions of the Park.

Introduction

The natural bushland areas of Kings Park formerly contained a open forest variously dominated by *Eucalyptus gomphocephala* DC. (tuart), *E. calophylla* Lindley (marri) and *E. marginata* Donn ex Sm. (jarrah). Over the past century this dominance by eucalypts has gradually given way to a low woodland consisting of *Allocasuarina fraseriana* (Miq.) L. Johnson (sheoak), *Banksia attenuata* R.Br. (slender banksia) and *B. menziesii* R.Br. (firewood banksia) (Beard 1967, Bennett 1988). The degradation appears correlated, in part, with frequent summer wildfires. In previous papers, it has been reported that this conversion to an open woodland of banksia and sheoak was due to the greater tolerance to fire (Main & Serventy 1956, Baird 1977) or the greater ability to compete for moisture (Beard 1967) of the sheoaks and banksias compared to the eucalypts, although no direct evidence was presented. Paradoxically, these authors also report that the banksias suffer the effects of fires less due to thick, hard bark compared to the sheoaks with their reported thin and rough bark, yet both species have successfully dominated the woodlands for at least the last thirty years when fires have been more frequent (Wycherley 1984).

On January 4, 1989, a very severe wildfire swept the central and southern regions of the Park (Fig 1), completely consuming the understorey and burning most of the canopy leaves and small branches. When resprouting from epicormic buds began to show following the fire, it appeared that many more trees failed to survive the fire than was expected from previous experience in the Park (Beard 1967, Baird 1977). In March, a section of burned

woodland was surveyed and mapped to assess the impact of the fire on the survival of trees in the Park. Subsequent re-surveys in September 1989 and May 1990 documented further changes to the original canopy structure of this region. The report presented here compares differences between species, diameter and height of the trees over these three surveys.

Methods

A belt transect of 41 quadrats of 10 m X 10 m was established between Winthrop Avenue and May Drive (Fig 1). In each permanently marked quadrat all stems greater than 4 cm were mapped, measured for diameter at breast height over bark and estimated for tree height. Stems were identified to species and in the case of *Allocasuarina fraseriana*, female trees with 'cones' were noted separately from the male and non-reproductive trees. Trees showing resprouting during the March sampling period were recorded as alive; all others were recorded as dead. During the winter, it was apparent that some of the trees, originally recorded as dead, were producing basal resprouts. Consequently, in September all trees were re-assessed for survival and the form of resprouting (stem, basal or both) was noted.

During the dry summer period, it was further noted that some trees that had initially resprouted had subsequently died, but there were additional trees, formerly assessed as dead but now showing basal resprouting. In May 1990, a third assessment of each tree provided categories of original fire deaths, deaths following some resprouting, survival as stem resprouters and survival as basal resprouts. All stems greater than 4.0 cm diameter at breast height (DBH) and over 2 m in height measured in March 1989 were assumed to constitute the original tree canopy population. The original population structure was assessed using size and height classes (8 cm and 1 m intervals, respectively). Analysis of Variance with Fisher's Least

Kings Park, Perth, Western Australia

Forrest Drive

Lovekin Drive

Arthur Fairall Playground

May Drive

Permanent Transect Line

Poole Avenue
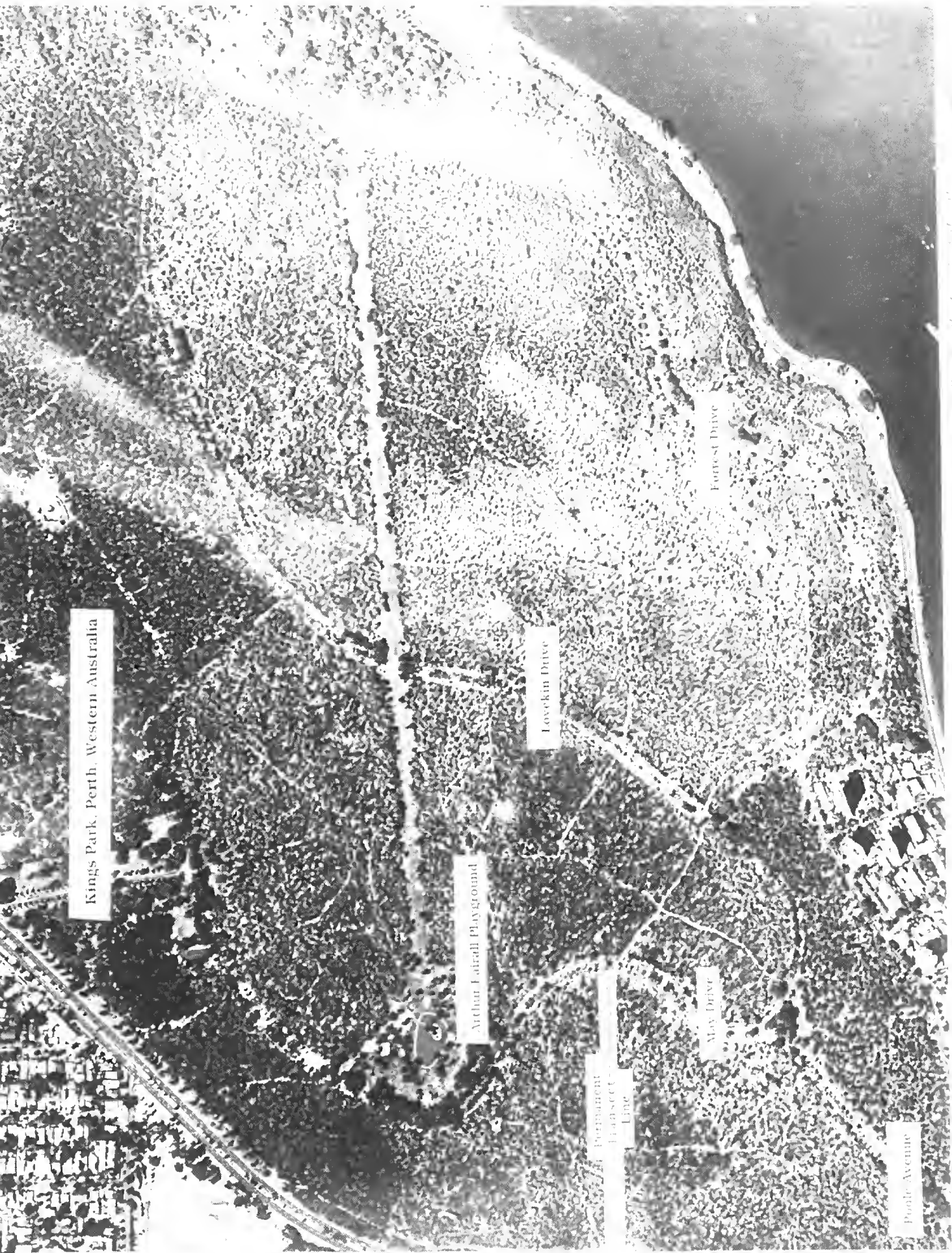
Significant Difference (LSD) was used to determine the statistical significance of the matrices of taxa classified initially by response category and subdivided by height and diameter.

Results

The tree population sampled in Kings Park in March 1989, indicated that the sheoak, *Allocasuarina fraseriana*, numbered more than 55% of the stems occurring in the sampling transect (Table 1). The three members of the genus *Banksia* made up 38% of the stems with *B. attenuata* contributing 30% of this total. The eucalypts in the transect at the present time numbered only 3% of the tree stem total.

A

All Trees

Diameter Class
(8 cm intervals from 0-80 cm)

B

All Trees

Height Class
(1 m intervals from 2.0-16.0 m)
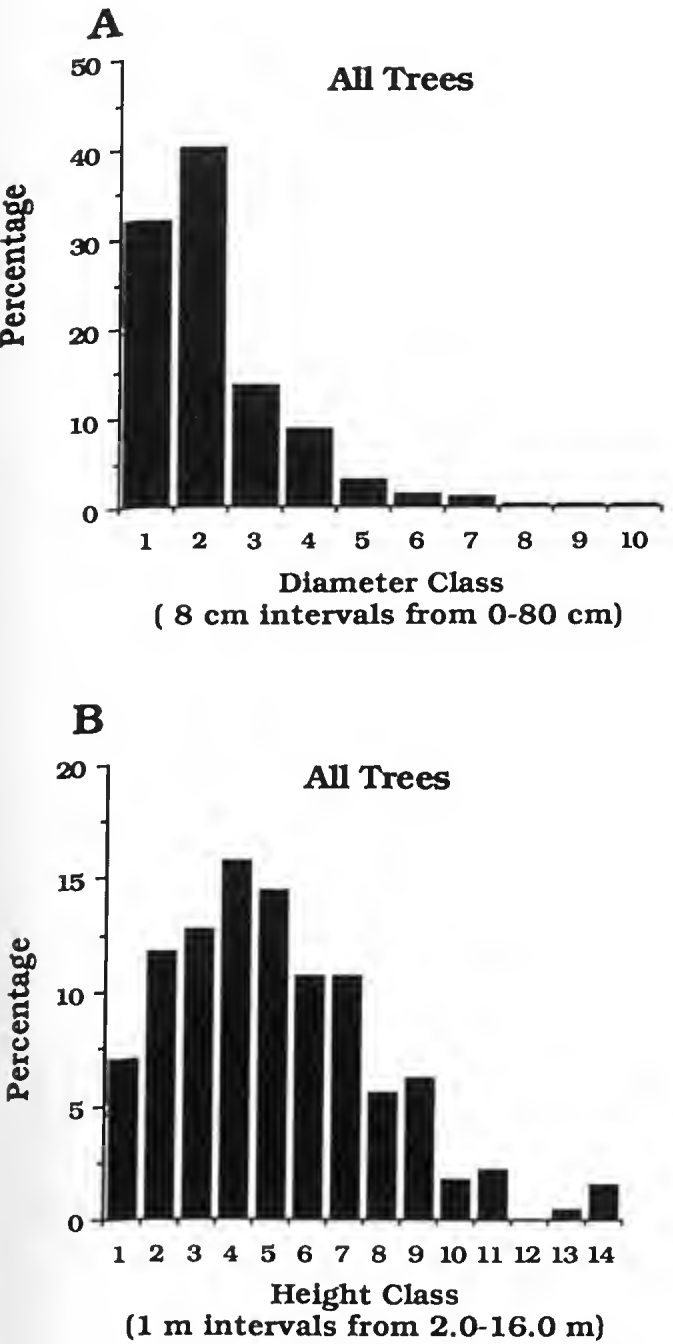
Figure 2. A Diameter class frequencies for diameter at breast height (classes of 8 cm beginning at 0 cm) and **B** height class frequencies (classes of 1 m beginning at 2.0 m) for the stem population in the Kings Park study transect of March 1989.

Table 1

Stem densities of trees in the Kings Park study transect in March 1989 (41 quadrats of 10 x 10 m)

Tree Taxa	Stems in transect	Stems per ha.	Relative Density %
A. fraseriana—Female	68	166	14.4
A. fraseriana—Male & Unknown Sex	195	476	41.3
Allocasuarina fraseriana— All stems	263	641	55.7
Banksia attenuata	140	341	29.7
B. grandis	7	17	1.5
B. menziesii	30	73	6.4
Eucalyptus gomphocephala	5	12	1.1
E. marginata	9	22	1.9
All other tree species	18	44	3.8
All trees	472	1,151	100.0

The patterns of diameter classes of the stems followed the typical negative exponential curve of frequency (Fig 2). Mean diameter for all trees was 14.0±0.5 cm. The somewhat reduced population of the first diameter (0-8 cm) class was caused by the limitation of 4 cm for the classification of trees for inclusion in the sample. The frequency of one metre height classes revealed a more poisson-like curve with a mean height of 6.2±0.1 m. Under the height and density system of Specht (1970), the vegetation prior to the fire would have been classified as a "low, open woodland".

The initial post-fire survey revealed that only 37% of the stems had resprouted in the three-month interval since the fire (Table 2). In the subsequent 6 months to September the total had risen to 61%, finally reaching a total stem survival record of 68% in May 1990. Although the initial record indicated that there was little difference between the survival of sheoaks and the banksias, the final record indicated that only 51% of the original banksia stems had resprouted by May 1990 compared to 82% for *Allocasuarina*. The remaining species, which included the eucalypts, fared even more poorly with only a 41% survival value 16 months following the wildfire. As with the she-oaks, 30-40% of the original stand of this group was recorded as dead at the first sampling, but subsequently produced resprouts.

The May 1990 assessment revealed that of the 33% of stems dead in the survey, most (29%) were killed directly by the fire; the remainder subsequently dying after having initally resprouted (Fig 3). About half (51%) of the original canopy population was reduced to basal sprouting individuals, with the remaining 16% as stem-resprouts. Compared to the partition for all stems, the better overall survival in *Allocasuarina fraseriana* was attributable to a greater ability to resprout from the base.

The division of sexes in *Allocasuarina* appeared to indicate that a greater proportion of females were killed by fire compared to the male and unreproductive category.

Table 2

Survivorship as judged by resprouting in the survey trees of Kings Park following the fire of 4 January 1989

Taxa	March 1989	September 1989	May 1990
All Trees	37%	61%	68%
Allocasuarina fraseriana	41%	77%	82%
All banksias	37%	41%	51%
All other species	6%	39%	41%
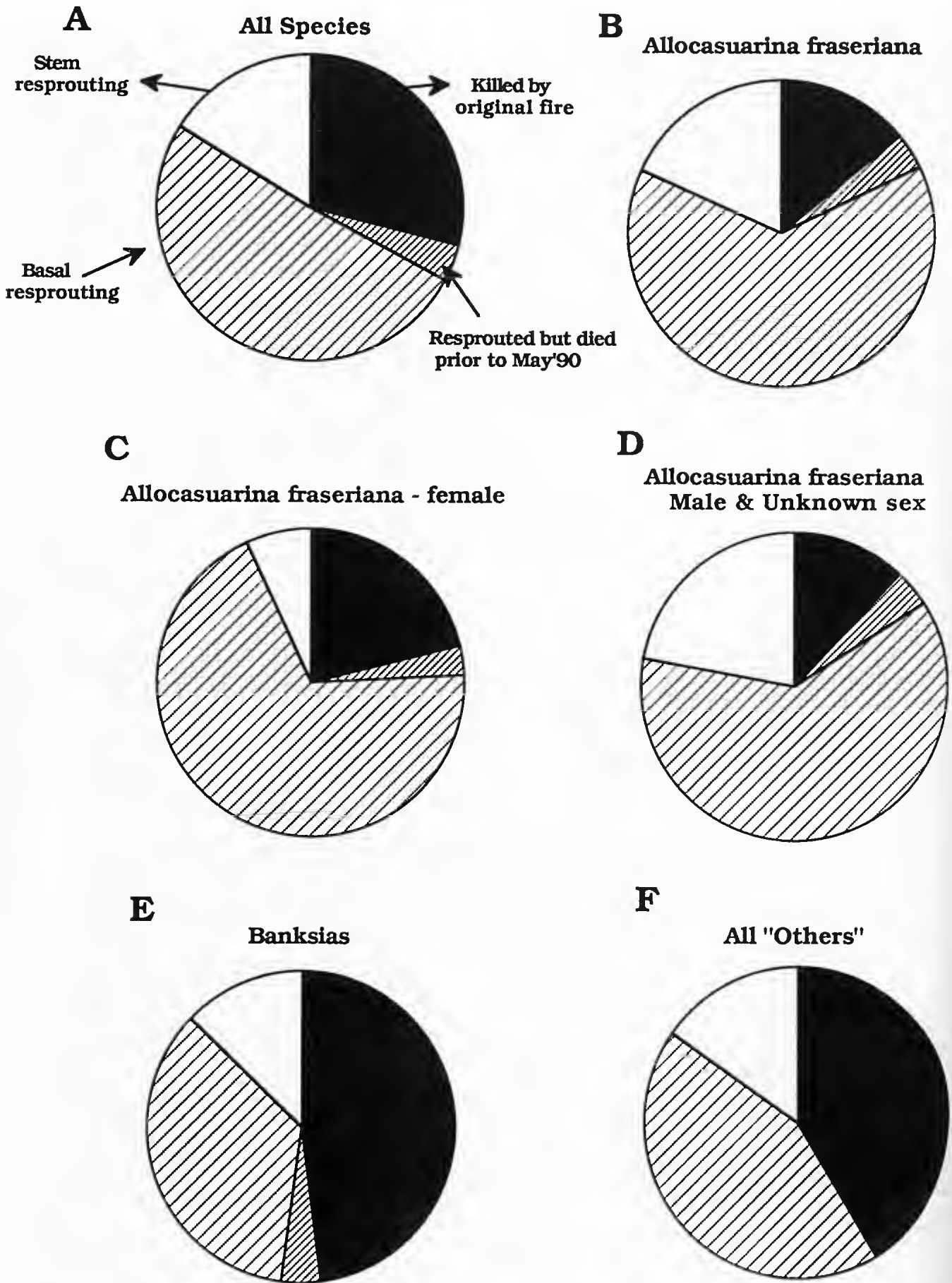
Figure 3. Proportions of stems of **A** All Species, *Allocasuarina fraseriana* (**B** all together and **C D** separated by sex), **E** the Banksias and **F** All "Other" species in the following categories: 1) Killed by the original fire; 2) Resprouting individuals which died prior to May 1990; 3) Stem resprouting individuals; and 4) Individuals with only basal resprouts.

However, this may be a spurious result since this latter category might be expected to contain stems which were genetically female, but did not carry fruit. The impact of the fire was generally greater on the banksias and the eucalypts with nearly half of their original populations of stems failing to resprout following the fire.

The analysis of variance revealed that the stems surviving the fire as basal resprouts only tended to be the smaller trees, both in diameter and height (Table 3). Also, the trees which initially resprouted but subsequently died were generally larger than those trees in the other categories. These trends were similar in all groups of taxa.

Discussion

The summer fire of January 1989 had a much more severe impact on the tree vegetation of Kings Park than had been observed following previous summer fires. Beard (1967) wrote "Both banksia and casuarina are hardy to fire and well withstand severe crown fires which destroy not only their leaves but the smaller branches as well." Baird (1977) was also impressed with the ability of the vegetation of Kings Park to survive fires, indicating that "none of the trees is fire-sensitive, all are capable of sprouting from epicormic buds although some suffer more damage than others." She also indicated that although none of the tree species were killed by fire, too frequent fires had a tendency to reduce certain species and that severe fires did kill the smaller saplings. Given these comments, the observed survival rates of only two out of every three trees following the latest severe fire, is clearly most unexpected.

The present study has unequivocally documented that the latest fire has had a drastic effect on the larger trees regardless of species. Under conditions of severe crown scorching it appears to be the smaller trees which have retained their ability to resprout and especially from basal epicormic buds. This is also somewhat unexpected since larger trees are presumed to have a greater underground store of living tissue, sources of dormant buds, and the water and nutrient reserve to nurture regeneration. There was no indication, however, that sheoaks suffer any more than banksias during severe fires, as previously suggested

(Main & Serventy 1957, Beard 1965, Baird 1977). In fact, sheoaks were the most tolerant of species, being reduced by only one-fifth, although all species were drastically affected.

The emergent eucalypt component of the tree canopy has been greatly altered by this severe fire. Another such fire could be expected to kill many of the remaining canopy trees leading to the resulting vegetation being more properly characterized as a shrubland with occasional emergent trees.

Richer and Serventy (1991) argue that the regeneration of eucalypts in Kings Park following fires of the 1930's was limited due to competition for summer moisture with the undergrowth of banksias and sheoaks. Seedlings of the banksias and sheoaks will also suffer in competition with the established resprouting shrubs and remaining trees, further restricting the number of trees in the region.

Hazard-reduction burning in the 1950s and 1960s accelerated the conversion of the vegetation from a eucalypt-dominated to a sheoak-dominated woodland in this area of Kings Park (Main and Serventy 1957, Beard 1967). The 1989 severe wildfire appears to have accelerated this process. Of interest, however, is that the direction of this successional change is in direct contrast to that proposed for *Eucalyptus/Casuarina* associations in eastern Australia based on paleogeographical evidence from Lake George (Singh and Geissler 1985). However, the Casuarinas referred to from the pre-historical Lake George habitat would be more like *Casuarina obesa* and not of the fire-tolerant *Allocasuarina fraseriana*-type.

The permanent transect of mapped trees established in this study will allow the documentation of further changes in the tree population structure in Kings Park in coming years. For example, seedling regeneration is being followed and is to be assessed as part of a separate study of sub-canopy level responses to the January 1989 fire. Maintenance and protection of Kings Park as an urban bushland is an important virtue for city residents and the majority of park users want the part left "undisturbed" (Johnson et al. 1974). Unfortunately, given the continued expectation of further vandal-lit fires in the park, it is more likely that tree numbers will continue to decline in this inner city bushland.

Table 3

Mean diameters and heights (±se) in May 1990 for response categories of trees in the Kings Park tree survey. Values within a category with different superscript letters are different at p<0.05 by Fisher's LSD.

Taxa	RESPONSE CATEGORY			
	Killed by Fire	Resprouted but died	Stem Resprouters	Basal Resprouters
DIAMETER (cm)				
All Stems	15.9±1.1[b]	24.9±3.6[a]	17.5±1.0[b]	11.0±0.5[c]
Sheoaks—all	21.3±2.5[b]	30.2±4.8[a]	17.8±1.4[b]	11.2±0.6[c]
Sheoaks—Female	27.8±4.5[b]	47.5±2.5[a]	23.7±5.6[b]	13.2±1.4[c]
Sheoaks—M.& U.	17.4±2.8[b]	26.7±5.6[a]	17.3±1.4[b]	10.5±0.7[c]
Banksias—all	13.7±1.1[a]	16.4±2.0[a]	16.4±1.1[a]	9.8±0.7[b]
All others	15.6±3.5[a]	—	10.5±3.1[a]	17.3±5.1[a]
HEIGHT (m)				
All Stems	6.4±0.3[b]	7.9±0.7[a]	7.5±0.3[a]	5.5±0.2[c]
Sheoaks—all	7.8±0.6[b]	8.8±0.8[a]	7.7±0.4[a]	5.6±0.2[c]
Sheoaks—Female	9.4±1.0[a]	12.0±0.1[a]	7.6±0.9[a]	5.5±0.3[b]
Sheoaks—M.& U.	6.8±0.7[a]	8.4±0.9[a]	7.6±0.4[a]	5.6±0.2[b]
Banksias—all	5.8±0.3[b]	6.1±0.7[ab]	7.0±0.5[a]	4.8±0.2[c]
All others	6.0±0.6[a]	—	6.0±2.0[a]	8.4±1.0[a]

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An overview of the ant fauna of Cape Arid National Park, Western Australia

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Abstract

This paper overviews the ant fauna of Cape Arid National Park (375-575 mm mean annual rainfall) in southwestern Australia, and compares it with that already described from Wyperfeld National Park (c. 400 mm) in northwestern Victoria. Ants were surveyed at 15 sites, primarily by pitfall trapping, during November 1988 and April 1989, with 141 species from 29 genera being recorded. Faunistic composition, in terms of the biogeographical affinities of species, the distribution of species across genera, the composition of species-groups within major genera, and the distribution of species across functional groups, was similar to that at Wyperfeld. Many species were common to both locations. The richest genera were *Camponotus* (28 species), *Iridomyrmex* (24 species) and *Melophorus* (15 species), as is typical of arid Australia. However, as is also the case at Wyperfeld, these genera included elements characteristic of more mesic regions, and Bassian genera such as *Prolasius*, *Notoncus*, *Colobostruma* and *Dolichoderus* contributed a significant proportion of species. The rich and distinctive Wyperfeld fauna, where Bassian elements are superimposed upon a typically arid assemblage, therefore appears to be characteristic of the mesic fringe (c. 400-500 mm mean annual rainfall) of semi-arid southern Australia.

Introduction

Semi-arid southern Australia supports some of the richest known ant faunas (Greenslade & Greenslade 1989), rivalling those of tropical lowland rainforests (Wilson 1959, 1987, Verhaagh 1990) which are generally considered to be the most diverse (Kuznezov 1957). Ant diversity is particularly high at Wyperfeld National Park (mean annual rainfall c. 400 mm) in the mallee region of northwestern Victoria, where a remarkable 138 species from 32 genera have been recorded from a 0.4 ha plot (Andersen 1983, Andersen & Yen 1985). This exceptional diversity can in part be explained by Wyperfeld's location on the mesic fringe of the southern arid zone, such that an already rich arid fauna is overlapped by taxa characteristic of cool-temperate (Bassian) Australia. The Wyperfeld fauna is typical of that occurring throughout the arid zone in having numerous species of *Iridomyrmex*, *Camponotus* and *Melophorus* (Greenslade 1979), but it also includes a sub-stantial number of Bassian elements (Andersen 1991a) such as species of *Prolasius*, *Notoncus*, *Dolichoderus*, *Colobostruma* and *Podomyrma*.

The extent to which the Wyperfeld fauna is typical of the mesic fringe of the southern arid zone is unknown, as ant faunas in these regions are poorly documented. This is especially true for southern Western Australia, where there appears to be no published account of any semi-arid fauna, despite the considerable work in more mesic regions (for examples see Majer 1982, Rossbach & Majer 1983, Majer *et al.* 1984, Majer & Brown 1986). This paper provides an overview of the ant fauna of Cape Arid National Park, located 120 km east of Esperance, Western Australia, and compares it with that at Wyperfeld.

Study Sites

Cape Arid National Park (c. 280,000 ha) experiences a warm to dry-warm Mediterranean climate with mean annual rainfall ranging from 375 mm (northern regions) to 575 mm (coastal southern region) (Bureau of Meteorology 1971, Beard 1975). Major substrates in the Park are Proterozoic granites and gneisses, mostly overlain with Pleistocene limestone deposits in the north and sands in the south, with Recent sands being common near the coast (Lowry & Doepel 1974). The Park is at the eastern extremity of the South-West Botanical Province, on the boundary with the semi-arid South-Western Interzone (Beard 1975, 1980).

Ants were surveyed at 15 sites, arranged in three clusters of five sites in the areas of Mt Ragged, Yokinup Bay and Seal Creek (Fig 1). A summary of the soils and vegetation at each site is provided in Table 1. The mallee woodlands are part of the Cooper vegetation system, the heaths part of the Esperance System, and the remaining types are within the Fanny's Cove System (Beard 1975).

Methods

Ants were sampled using pitfall traps (4.2 cm diameter plastic vials, partly filled with ethanol as a preservative), which provide useful quantitative information on the composition of ground-foraging ants in open habitats (Andersen 1983, 1991c) such as those at Cape Arid. Very few ant species in the Australian arid zone forage exclusively in soil or on vegetation (Greenslade 1979) and thereby avoid capture in pitfall traps. A line of 10 traps with 5 m spacing was located at each of the 15 sites, and operated for a 48 hr period during November 1988. Species

were also collected opportunistically by hand. The weather was mostly fine, but with some drizzle at Mt Ragged. Maximum temperatures ranged from about 25-30°C, with temperatures being lowest during the Mt Ragged sampling period. The survey was repeated at Mt Ragged (sites 4 and 5 only) during warm weather in April 1989.

The sampling regime was designed to provide a broad coverage of the regional fauna, rather than detailed information for particular sites. Site comparisons were therefore not attempted. Most ant species in southern Australia are at or near their peak activity during November, although some species forage exclusively during winter months (Andersen 1983, 1986). Aside from the latter species, the survey was therefore likely to provide a reasonable overview of the Cape Arid fauna.

Ants were sorted to species, but the poor species-level taxonomy of Australian ants meant that only a small proportion could be named with certainty. Some other species were given names prefaced by a question mark (for example *Brachyponera ?lutea*) to indicate that the taxa require further study before they can be identified with certainty. Where possible, the remaining species were assigned to informal species-groups according to Andersen (1991a): such species are denoted by inverted commas, for example *Rhytidoponera 'metallica'*. Otherwise, unidentified species were given letter codes that apply only to this study. A full collection of voucher specimens is held by the senior author.

Patterns of community organization were examined by classifying species into functional groups according to their habitat requirements and competitive interactions. This classification is modified from Greenslade (1978), and has been widely discussed and applied elsewhere (see Andersen 1990, 1991b). There are seven groups: 1. Dominant Dolichoderinae (primarily species of *Iridomyrmex*),

Table 1

Soils and vegetation at study sites in Cape Arid National Park.

Site	Soil	Vegetation
Mt Ragged		
1	calcareous loam/limestone	mallee woodland
2	calcareous loam/limestone	mallee woodland
3	lateritic podzol	heath
4	siliceous sand	*Banksia* woodland
5	calcareous loam/limestone	mallee woodland
Yokinup Bay		
1	calcareous sand	dune shrubland
2	siliceous sand	*Banksia* woodland
3	dark loam	eucalypt woodland
4	sand over clay	heath
5	gravelly sand over clay	heath
Seal Creek		
1	sand over laterite	heath
2	siliceous sand	heath
3	sand over clay	heath
4	gravelly sand over clay	heath
5	siliceous sand	dune shrubland

which are highly active and aggressive species exerting a strong influence on other ants (Greenslade 1976, Andersen 1992 *in press*); 2. Associated subordinate Camponotini (primarily species of *Camponotus*), which appear to co-exist successfully with species of *Iridomyrmex* due to their submissive behaviour, and to differences in body size and time of foraging; 3. Climate specialists: either (a) Bassian taxa (for example species of *Prolasius* and *Notoncus*) which occur predominantly in cool and wet regions, where the abundance of *Iridomyrmex* is generally low; or (b) specialized arid-adapted taxa (for example species of *Melophorus* and *Meranoplus*); 4. Cryptic and Sub-cryptic species, which forage exclusively or primarily within soil and litter; 5. Opportunists (primarily species of *Rhytidoponera*, *Paratrechina* and *Tetramorium*) which are unspecialized species with poor competitive ability that are often characteristic of disturbed sites (Andersen & McKaige 1987, Andersen & Burbidge 1991); 6. Generalized Myrmicinae (species of *Crematogaster*, *Monomorium* and *Pheidole*), which are unspecialized myrmicine species that are successful members of Australian ant communities because of their rapid recruitment and ability to defend food resources (Andersen *et al.* 1991, Andersen 1992 *in press*); and 7. Large/Solitary foragers (for example species of *Myrmecia*) which, due to their large size and low densities, do not interact greatly with other ants.

Results

Faunistic Composition

A total of 141 species from 29 genera were collected (a species list is included as an Appendix). This is by no means the complete regional fauna, as the species accumulation curve (Fig 2) continues to rise, and 64 (45%) of the species were recorded at only one site. The high turnover of species across sites can be attributed to a combination of the relatively low sampling intensity at each site, and the patchy distribution of species (see Table 3 for examples of the latter). This makes it impossible to give a reliable estimate of the total number of species in the region.

The mean number of species per genus (4.9) is similar to that at Wyperfeld (4.6), and falls between that of more mesic (for example 2.9 at Kangaroo Island, SA; 550 mm mean annual rainfall) and more arid (for example 6.3 at
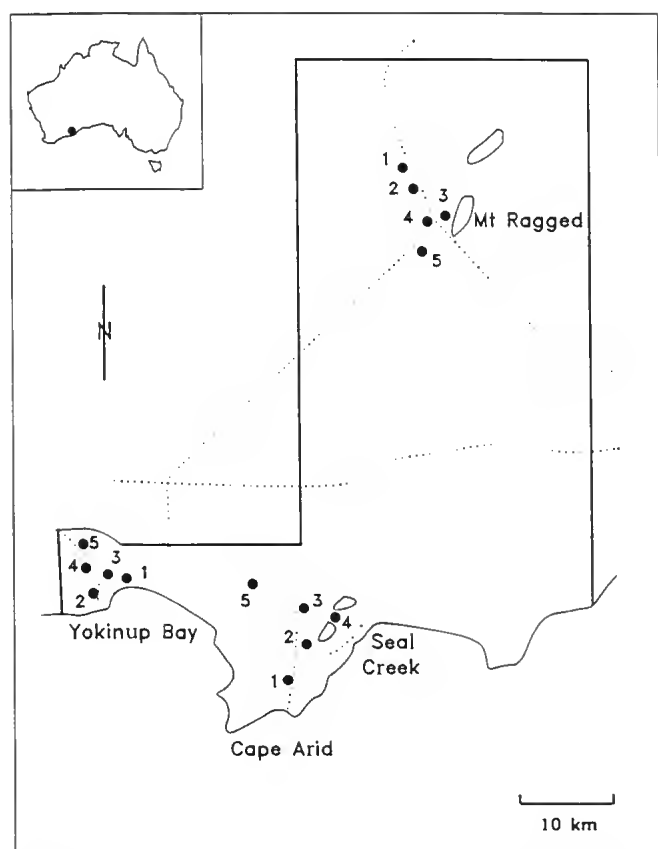
Figure 1. Location of study sites (●) in Cape Arid National Park, W.A.

Table 2

Ant community organization at Cape Arid (present study) compared with Wyperfeld (Andersen 1983, 1984, Andersen & Yen 1985; heath and mallee sites combined, pitfall trap data only). Taxa are classified into functional groups (see text), and data are total numbers of species recorded (including hand collections) and, in brackets, mean percentage abundance in pitfall traps (excluding hand collections) during November. The Cape Arid sites have been grouped according to their location in the Mt Ragged (MR), Yokinup Bay (YB) or Seal Creek (SC) areas. Some genera were found at Wyperfeld but not at Cape Arid; these are listed as 'other' and are included in Wyperfeld species totals.

Category/Genera		Cape Arid			Wyperfeld
	MR	YB	SC	TOTAL	
1. DOMINANT DOLICHODERINAE					
Iridomyrmex	6(43)	11(48)	6(54)	19(49)	13(35)
Other	—	—	—	—	2
Sub-total	6(43)	11(48)	6(54)	19(49)	15(35)
2. ASSOCIATED SUBORDINATE CAMPONOTINAE					
Camponotus	9(5)	16(7)	9(9)	28(7)	29(2)
Notostigma	0	0	1(<1)	1(<1)	0
Polyrhachis	2(<1)	2(<1)	1(<1)	3(<1)	5(<1)
Sub-total	11(5)	18(7)	11(9)	32(7)	34(2)
3. CLIMATE SPECIALISTS					
(a) Cold Climate Specialists					
Colobostruma	0	0	1(<1)	1(<1)	2(<1)
Dolichoderus	1(0)	1(0)	0	1(0)	3(<1)
Notoncus	2(0)	1(2)	2(1)	4(1)	3(<1)
Prolasius	0	1(<1)	1(1)	2(<1)	1(<1)
(b) Hot Climate Specialists					
Adlerzia	0	1(<1)	0	1(<1)	1(<1)
Anisopheidole	0	0	1(<1)	1(<1)	1(<1)
Cerapachys	0	1(1)	1(<1)	2(<1)	2(<1)
Melophorus	8(<1)	8(9)	3(<1)	15(3)	13(8)
Meranoplus	3(11)	1(<1)	2(1)	5(4)	3(1)
Monomorium ('*Chelaner*')	2(1)	2(<1)	3(4)	6(2)	4(<1)
Other	—	—	—	—	6
Sub-total(a + b)	16(12)	16(13)	14(8)	38(11)	39(9)
4. CRYPTIC OR SUB-CRYPTIC SPECIES					
(a) Cryptic Species					
Brachyponera	1(0)	0	1(<1)	1(<1)	1(<1)
Solenopsis	0	1(<1)	1(<1)	2(<1)	1(<1)
Acropyga	1(0)	0	0	1(0)	1(<1)
(b) Sub-cryptic Species					
Bothriomyrmex	1(0)	1(0)	0	1(0)	0
Iridomyrmex '*darwinianus*'	2(2)	1(2)	1(6)	3(3)	1(9)
Plagiolepis	0	0	2(<1)	2(<1)	2(<1)
Stigmacros	1(0)	3(1)	0	3(<1)	13(2)
Tapinoma	1(0)	1(<1)	0	1(<1)	0
Other	—	—	—	—	2
Sub-total(a + b)	7(2)	7(4)	5(6)	14(4)	21(11)
5. OPPORTUNISTS					
Aphaenogaster	1(10)	0	0	1(3)	1(<1)
Iridomyrmex '*glaber*'	2(0)	0	0	2(0)	2(<1)
Rhytidoponera	2(12)	2(4)	1(4)	3(7)	0
Tetramorium	2(0)	1(1)	2(<1)	3(<1)	2(<1)
Sub-total	7(22)	3(5)	3(4)	9(10)	5(<1)
6. GENERALIZED MYRMICINAE					
Crematogaster	3(9)	1(<1)	0	6(3)	6(3)
Monomorium	5(2)	7(20)	1(2)	8(8)	8(35)
Pheidole	2(4)	1(3)	1(12)	4(6)	6(4)
Sub-total	10(15)	9(23)	2(14)	18(17)	20(42)
7. LARGE, SOLITARY FORAGERS					
Myrmecia	1(0)	5(2)	2(2)	9(1)	4(<1)
Platythyrea	1(0)	0	1(0)	2(0)	0
Sub-total	2(0)	5(2)	3(2)	11(1)	4(<1)
TOTAL	59(100)	69(100)	44(100)	141(100)	138(100)

Table 3

Distribution of *Iridomyrmex* species across sites. Data are numbers of ants recorded in pitfall traps during November (dashes indicate zero records).

	Mt Ragged					Yokinup Bay					Seal Creek				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Iridomyrmex sp A	—	—	19	—	1	29	—	—	98	147	—	163	—	—	—
I. 'bicknelli' sp A	—	—	—	—	—	—	—	—	—	—	—	—	—	54	14
I. 'bicknelli' sp D	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
I. 'conifer' sp A	43	—	—	65	—	79	—	—	—	—	—	—	—	—	—
I. 'conifer' sp B	—	—	—	—	—	—	507	—	19	—	110	92	—	58	28
I. 'conifer' sp C	—	—	—	—	—	—	—	—	—	—	—	66	76	25	—
I. 'dromus' sp B	—	—	—	6	—	—	—	1	—	—	—	—	—	—	—
I. 'gracilis' sp A	3	77	6	—	—	20	—	3	—	1	—	—	—	—	—
I. 'itinerans' sp A	—	—	—	—	—	—	—	28	—	20	—	—	—	—	—
I. 'purpureus'	—	—	—	—	—	5	1	—	5	2	—	—	—	1	7
all others	—	9	—	—	—										

Cambrai, SA; 350 mm) sites (data from Greenslade & Greenslade 1989). The richest genera were *Camponotus* (28 species), *Iridomyrmex* (24 species) and *Melophorus* (15 species), as is typical of the Australian arid zone. These three genera together comprised 47% of total species, compared with 42% at Wyperfeld. They typically comprise a greater proportion of species at more arid sites (for example, 62% at Cambrai), and a lesser proportion at more mesic sites (for example, 31% at Kangaroo Island).

The overlap of Bassian and Eyrean (arid) taxa that is distinctive of Wyperfeld also occurs at Cape Arid. At Cape Arid, 27% of the species belong to Eyrean taxa, 16% to Bassian taxa, and the remainder (57%) to widespread taxa (see Appendix). These figures are almost identical to those at Wyperfeld: 28%, 17% and 55% respectively. As at Wyperfeld, Cape Arid supports Bassian taxa such as *Iridomyrmex* 'itinerans', *Camponotus* 'innexus' and species of *Notoncus*, *Prolasius*, *Dolichoderus* and *Colobostruma*. More generally, the Cape Arid fauna is very similar to that at Wyperfeld at the species-group level. For example, the major species-groups of *Iridomyrmex* at Cape Arid were 'bicknelli', 'gracilis', 'dromus', 'darwinianus' and 'itinerans', as they are at Wyperfeld, and the same goes for the 'claripes', 'ephippium' and 'ceriseipes' groups of *Camponotus*. Indeed, many species collected at Cape Arid appear to be identical to those from Wyperfeld, including *Brachyponera ?lutea*, *Adlerzia froggatti*, *Anisopheidole antipodum*, *Notostigma sanguinea*, *Aphaenogaster ?barbigula*, and *Camponotus whitei*.

Community Organization

Dominant species of *Iridomyrmex* contributed about half of the total ants in traps (Table 2), with individual species distributed patchily across (Table 3) and within (Table 4) sites. Each of the three areas sampled supported a distinctive suite of *Iridomyrmex* species. Within the *conifer* group, for example, sp A was found only in the Mt Ragged area (Table 3). Species of 'conifer' were abundant at nine of the 15 sites, with two species never recorded together. *Iridomyrmex* 'bicknelli' sp. D was only recorded at Seal Creek sites, *I.* 'itinerans' and *I.* 'purpureus' only at Yokinup Bay sites, and all but one specimen of *I.* 'gracilis' sp. A was recorded at Mt Ragged sites. Of the eleven common species, only *Iridomyrmex* sp A was found at all three groups of sites. Patchiness of *Iridomyrmex* species was also pronounced within sites. At Mt Ragged site 5 during April, for example, species of *Iridomyrmex* were recorded in all traps, but individual species tended to be mutually exclusive (Table 4).

The overall abundance of dominant *Iridomyrmex* at each site exhibited a humped relationship with total species richness (Fig 3). If it is assumed that the abundance of *Iridomyrmex* reflects environmental favourability for ants (Andersen 1992 *in press*), then this pattern is consistent with the suppression of diversity by dominant species under favourable conditions, following the Grime (1973), Connell (1978) and Tilman (1982) models of the control of local
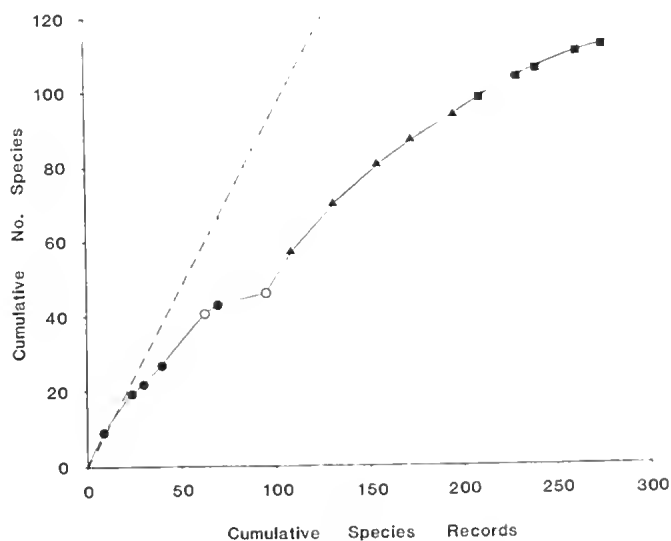
Figure 2. Species accumulation curve based on pitfall catches (● Mt Ragged sites, November;   Mt Ragged sites April; ▲ Yokinup Bay sites, ■ Seal Creek sites). The dashed line represents the situation where every species record is different.

Table 4

Distribution of *Iridomyrmex* species in individual pitfall traps at Mt Ragged site 5 during April 1989 (dashes indicate zero records).

	Trap No.									
	1	2	3	4	5	6	7	8	9	10
Iridomyrmex sp A	5	—	1	—	10	—	—	—	—	—
I. 'bicknelli' sp A	—	4	—	—	—	23	—	—	—	12
I. 'gracilis' sp A	—	—	1	6	21	—	50	50	36	—

diversity in communities of plants and sessile marine invertebrates. Humped diversity patterns in ant communities, caused by competition from *Iridomyrmex*, have been previously documented at tuna baits in northern Australia (Andersen 1992 *in press*).

Associated subordinate Camponotini (total of 35 species, mostly belonging to *Camponotus*) and climate specialists (38 species, mostly belonging to *Melophorus*, *'Chelaner'* and *Meranoplus*) together contributed exactly half of the total species recorded, but represented less than 20% of ants collected in traps. The four truly cryptic species recorded (*Acropyga* sp., *Brachyponera ?lutea* and two species of *Solenopsis*) were each represented by a single individual in traps. Species of the *darwinianus* group of *Iridomyrmex* were locally common, especially in the Seal Creek area, but other sub-cryptic species were only rarely recorded. The most common opportunist was *Rhytidoponera 'metallica'*, which was recorded at 12 of the 15 sites. Generalized myrmicines averaged 17% of total ants in traps, but different genera predominated in the three areas: *Crematogaster* at Mt Ragged sites, *Monomorium* at Yokinup Bay sites, and *Pheidole* at Seal Creek sites. Nine species of *Myrmecia* (Large/Solitary foragers) were recorded, but they comprised only about 1% of total pitfall catches.

Pitfall trap data are also available for Wyperfeld (Table 2). In terms of numbers of species, the functional group profiles of the two locations are very similar, except far fewer species of Large/Solitary foragers were recorded at Wyperfeld (4) than at Cape Arid (11). The relative abundance of dominant *Iridomyrmex* at Cape Arid was somewhat higher than at Wyperfeld (49% compared with 35%), and generalized myrmicines substantially lower (17% compared with 42%). In particular, the very high abundance of *Monomorium* recorded at Wyperfeld (35% total ants in traps) was observed at only one of the 15 Cape Arid sites.

Discussion

Comparisons between the ant faunas of Cape Arid and Wyperfeld are constrained by major differences in sampling area and intensity: at Cape Arid a large area was surveyed at a low intensity, whereas the reverse was true at Wyperfeld. This makes it impossible to compare species richness at the two locations, and difficult to interpret differences in the relative abundances of major taxa. For example, it is not known if the high abundance of *Monomorium* at Wyperfeld is representative of the region as a whole, or is peculiar to the site studied. Similarly, the fewer species of Large/Solitary foragers recorded at Wyperfeld reflects the small area sampled.

However, the data do allow for broad comparisons of faunistic composition. Like Wyperfeld, Cape Arid National Park supports a rich ant fauna composed of a framework of arid zone taxa which is overlapped by a broad range of Bassian elements. (Interestingly, a mixing of Bassian and arid zone taxa is also evident in the vascular plants and vertebrate animals at Cape Arid, but in these groups it is the Bassian taxa which predominate [A H Burbidge, G J Keighery, J K Rolfe & J J Alford, unpublished data]). Moreover, faunistic composition is similar at the two locations at the species-group level, and also in terms of the distribution of species across functional groups. There is, however, at least one important compositional difference: the *conifer* group of *Iridomyrmex* was a major component of the Cape Arid fauna, but does not occur at Wyperfeld (it is endemic to southwestern Australia). Three species of the group were recorded in the present study: they were among the most abundant ants collected, and appear to be the leading dominant ants in the region (Table 3). Their nest mounds were a conspicuous feature of the landscape, particularly on well-drained sandy soils.

The similarity of the Cape Arid ant fauna to that at Wyperfeld suggests that the rich and biogeographically distinctive Wyperfeld fauna is characteristic of the semi-arid/sub-humid zone (*c.* 400-500 mm mean annual rainfall) throughout much of the southern fringe of arid Australia. However, a major question remains to be addressed: just how diverse is the ant fauna of semi-arid southern Australia? Some species appear to occur throughout the region, but far more information is required on the distributions of other species before we can know if the answer is many hundreds or thousands of species.

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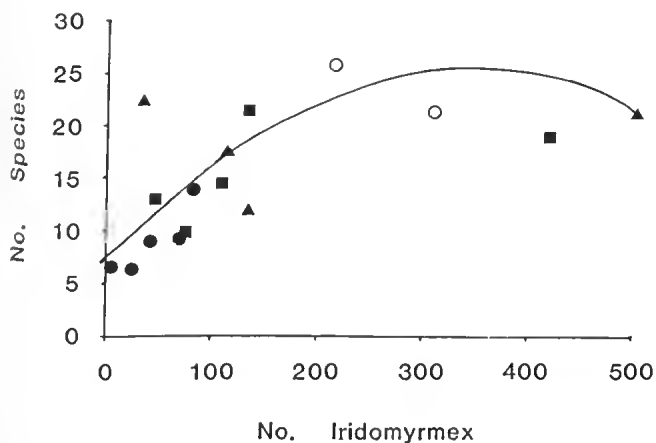
Figure 3. Relationship between total number of species and the abundance of dominant *Iridomyrmex* recorded at each site (symbols as in Fig 2). The regression equation is y = 8.0 + 0.09x − 0.0001x^2, r^2 = 0.51. The quadratic model gives a greater r^2 than either linear (r^2 = 0.35) or logarithmic (r^2 = 0.40) models.

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Appendix

List of ant species recorded at Cape Arid National Park, WA. Authorities for species names are given in Taylor and Brown (1985). The biogeographical affinities (E = Eyrean; B = Bassian; W = widespread) of each species is given in brackets.

Myrmeciinae

Myrmecia analis (W), *M. chasei* (W), *M. clarki* (W), *M. ?mandibularis* (W), *M. vindex* (W), *M. ?decipiens* (W), *M.* sp. nr. *swalei* (W), *M. ?tepperi* (W), *M.* sp. nr. *urens* (W).

Ponerinae

Brachyponera ?lutea (W); *Cerapachys gilesi* (W); *Cerapachys incontentus* (E); *Platythyrea dentinodis* (B), *P. micans* (B); *Rhytidoponera* sp. nr. *anceps* (W); *R. 'metallica'* (W), *R. punctata* (W).

Myrmicinae

Adlerzia froggatti (E); *Anisopheidole antipodum* (E); *Aphaenogaster ?barbigula* (W); *Colobostruma ?cerornata* (B); *Crematogaster* spp (x 5;W); *?Mayriella* sp. (B); *Meranoplus* spp (x 5;E); *Monomorium* ('Chelaner') spp (x 6;E,B), other *Monomorium* spp (x 8;W); *Pheidole* spp (x 4;W); *Solenopsis* spp (x 2;W); *Tetramorium* spp (x 3;W).

Dolichoderinae

Bothriomyrmex sp. (W); *Dolichoderus 'scabridus'* (B); *Iridomyrmex 'bicknelli'* (4 spp;W), *I. 'conifer'* (3 spp;W), *I. 'darwinianus'* (3 spp;W), *I. 'dromus'* (4 spp;E), *I. 'glaber'* (W), *I.* sp. nr. *glaber* (W), *I. 'gracilis'* (3 spp;W), *I. 'itinerans'* (B), *I.* sp. nr. *purpureus* (E), other *Iridomyrmex* spp (x 3;W); *Tapinoma 'minutum'* (W).

Formicinae

Acropyga sp (W); *Camponotus 'ceriseipes'* (3 spp;E), *C. 'ephippium'* (4 spp;E), *C. 'innexus'* (2 spp;B) *C. 'intrepidus'* (B), *C. 'nigriceps'* (E), *C. 'rubiginosus'* (2 spp;W), *C. 'testaceipes'* (2 spp;B), *C. ?whitei* (E), other *Camponotus* spp (12 spp;W); *Melophorus* spp (x 15;E); *Notoncus 'enormis'* (3 spp;B), *N. 'gilberti'* (B); *Notostigma sanguinea* (W); *Plagiolepis* spp (x 2;W); *Polyrhachis ?perthensis* (B), *P.* sp. nr. *patiens* (B), *P.* ('Campomyrma') sp(B); *Prolasius* spp (x 2;B); *Stigmacros* ('Campostigmacros') spp (x 2;W), *S.* ('Stigmacros') sp (W).

Seed release from *Banksia baxteri* and *Hakea crassifolia* following scrub-rolling and burning

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Abstract

Seed release patterns were compared for standing and felled plants of two serotinous shrubs, *Banksia baxteri* and *Hakea crassifolia*, including plants of each species burnt 18 days after felling. Standing plants of both species released only a small proportion of their seed store during the 11 month period of the study. Burning resulted in high levels of follicle rupture and seed release for felled *B. baxteri*; felled but unburnt plants did not release significant amounts of seed despite progressive desiccation. *H. crassifolia* follicles on felled stems opened readily after burning, but also opened in the absence of fire. A laboratory study indicated that the rate of follicle opening was strongly related to the severity of drying conditions.

Fuel reduction burning of shrublands in south-western Australia is sometimes preceded by scrub-rolling: both operations may affect the regeneration of shrubland plant species. Seed released from felled stems in the period between scrub-rolling and subsequent burning may be damaged by heat or even incinerated, thereby reducing the seed bank available for regeneration. The potential for such seed losses can be minimised by keeping the period between scrub-rolling and burning short, preferably no more than a few weeks.

Introduction

Many species of Proteaceae from the shrublands of south-western Australia accumulate seed in woody fruits in the canopy of mature plants; such species are termed serotinous (Lamont 1991). This trait is characteristic of a number of species of *Banksia*, *Hakea*, *Dryandra* and *Xylomelum* (Bell *et al.* 1987, Bellairs & Bell 1990). Fruit opening and subsequent seed release may be stimulated by a variety of mechanisms that promote desiccation of the abscission zone, including heat, and death of the branch or plant (Lamont 1991). The importance of heat in follicle rupture on serotinous *Banksia* species has been well documented (Gill 1976, Bradstock & Myerscough 1981, Lamont & Cowling 1984, Enright & Lamont 1989a).

Shrublands in south-western Australia are sometimes scrub-rolled in advance of fuel reduction burning. Scrub-rolling facilitates prescribed burning by creating a more continuous fuel-bed and increasing the proportion of dead fuel through the curing of foliage on felled stems. Fires are more readily controlled in scrub-rolled fuels because flame heights are reduced; this is of considerable importance where narrow buffer strips (typically 100-200 m wide) are to be burnt around the perimeter of a bushland reserve.

Seed released from follicles on felled stems in the period between scrub-rolling and subsequent burning may be damaged by heat or even completely incinerated, thereby reducing the quantity of seed available for regeneration (Richardson & van Wilgen 1986). This may lead to a decline in the population density of species that do not resprout after fire or maintain a seed store in the soil. Knowledge of seed release characteristics is therefore valuable for identifying species which may be vulnerable to this type of disturbance.

We studied seed release from two serotinous shrubs that commonly occur together in shrubland communities on the southern sandplain of Western Australia. *Banksia baxteri* R. Br. produces squat cones with up to 6 follicles, each containing two seeds (George 1981). Florets may persist on cones for several years after maturity. *Hakea crassifolia* Meissn. has a spherical woody follicle about 5 cm in diameter that splits symmetrically, releasing two seeds with membranous wings. The aim of the study was to compare the rate and extent of follicle opening and seed release on felled stems of these two species, both with and without the influence of fire; a control group of standing, unburnt plants were also examined. Such information provides a basis for management guidelines designed to maintain seed banks of serotinous species in scrub-rolled buffer strips.

Methods

The study was undertaken in mallee heath shrubland (Beard 1979) near Two Mile Lake (34° 29' S, 118° 15' E) in the Stirling Range National Park, Western Australia. The area experiences a mediterranean climate with cool moist winters and warm dry summers. At Mt Barker, about 55 km south-west of the site, mean daily maximum and minimum temperatures are 27.2 °C and 13.5 °C respectively in the hottest month (January), and 14.7 °C and 6.4 °C respectively in the coldest month (July). Mean annual rainfall is 472 mm at Kojaneerup, about 10 km from the study site. The area selected for study had been unburnt for 20 years and was dominated by 2-3 m tall thickets of *B. baxteri* with scattered 3-4 m tall *H. crassifolia*, both species growing as open-branched shrubs.

A 100 m wide strip was scrub-rolled through part of the site on 21 March 1989 (Day 0); within this strip a 0.25 ha plot was demarcated and excised from later burning operations. During the initial assessment on 30 March (Day 9) we selected felled plants of *B. baxteri* (10 in the main strip, 10 in the excised plot) and *H. crassifolia* (2 in the main strip); the low density of the latter species at the site prevented more extensive sampling. Standing shrubs of *B.*

Table 1

Numbers of plants, cones and follicles for *B. baxteri* in each treatment.

Treatment	No. of plants	No. of cones	Total No. of follicles
Standing	8	41	116
Felled/unburnt	10	43	93
Felled/burnt	10	39	83
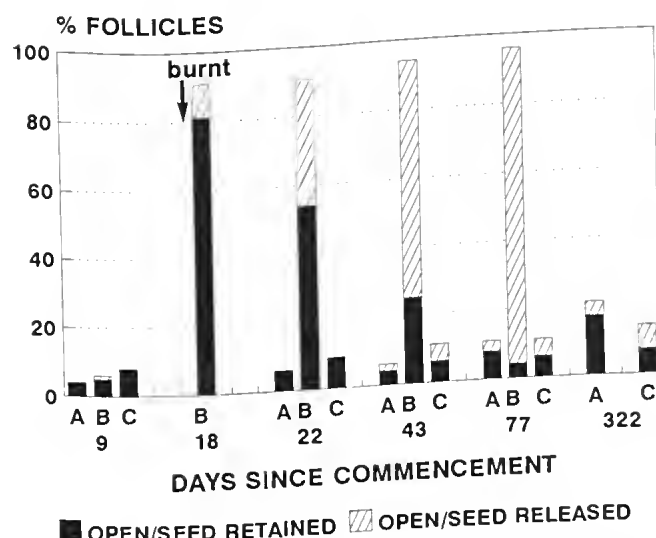
Figure 1 Condition of follicles on *B. baxteri* cones for three treatment groups: (A) felled/unburnt, (B) felled/burnt, and (C) standing/unburnt. Scrub-rolling took place on Day 0. Felled/burnt plants were examined two hours after burning on Day 18.
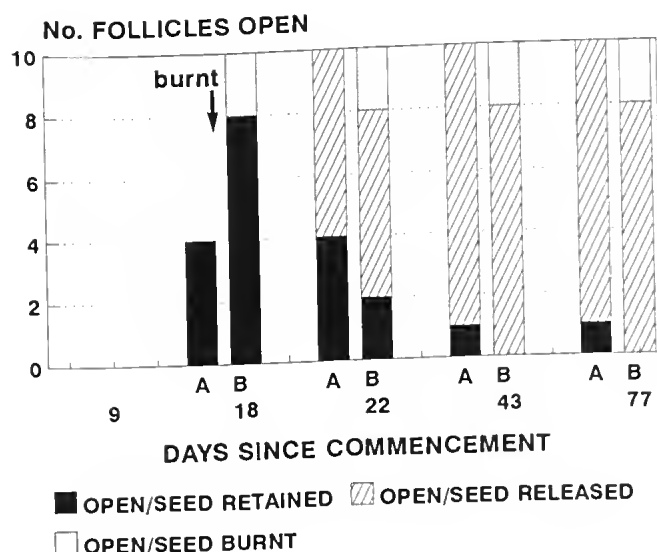
Figure 2 Condition of follicles on felled stems of *H. crassifolia*: (A) for the stem with the intact root system, and (B) for the severed stem. On Day 18 follicles were examined two hours after burning.

baxteri (8) and *H. crassifolia* (2) were also selected in the adjacent untreated area. Each of the *H. crassifolia* plants carried ten mature, unopened follicles at the commencement of the study. One-year-old *B. baxteri* cones on each stem were identified with numbered aluminium tags and the condition of individual follicles described; if open, note was made as to whether the seed was retained or released. Numbers of cones and follicles for each treatment group are shown in Table 1.

The main scrub-rolled strip was burnt during mild conditions on 8 April (Day 18) at about 1500 hrs. About 90% of the ground litter and foliage on felled stems was consumed by the fire which generated intensities (Byram 1959) of 300-500 kW/m. The condition of individual follicles on felled stems within this strip was examined 2 hours after burning, and a small number that had not been burnt were excluded from further study. Plants in all treatment groups were examined again on Day 22 and then at approximately monthly intervals until June when assessment of plants in the burnt strip ceased because seed release was largely complete. Final assessment of plants that had been felled but not burnt, and those in the undisturbed area took place in February 1990 (Day 322).

In October 1990, 28 *B. baxteri* cones were collected at random from each of the standing and felled/unburnt groups of plants. Seed was extracted by heating the cones with a blowtorch to open the follicles, and the seed collected was then placed on moistened vermiculite in petri dishes and maintained at 12-15 °C. The number of germinants was scored after 50 days.

To supplement the limited field data on the opening of *H. crassifolia* follicles in the absence of fire, samples of 23 follicles were dried in the laboratory under three regimes of temperature (T, °C) and relative humidity (RH, %), as follows:

(A) T=35, RH=20
(B) T=25, RH=40 and
(C) T=15, RH=60.

Treatments were imposed within 24 hours of follicles being harvested in the field.

Results

B. baxteri

At the commencement of the experiment more than 90% of the follicles in each treatment group were closed, and the small proportion that were open generally still contained seed. The scrub-rolling operation resulted in the complete severing of the root systems on all felled *B. baxteri*, a reflection of the brittle character of stem tissues.

Fire stimulated the rupture of follicles, and within 2 hours of being burnt more than 90% of follicles on felled stems had opened (Fig 1). By Day 77, fifty nine days after burning, the proportion of follicles opened had increased to 96%. The small number that failed to open typically showed signs of damage by cockatoos and insect borers. Seed was progressively released from opened follicles between April and June and less than 5% of open follicles still retained seed by Day 77 (Fig 1).

By contrast, few follicles on unburnt cones opened between March 1989 and February 1990, irrespective of whether the cones were on standing or felled stems (Fig 1). At the completion of the experiment the proportion of opened follicles on cones in the felled treatment (21%) was not significantly different from that of standing trees (14%) (Chi squared = 1.87, P > 0.05).

The number of intact seeds recovered from cones collected in October 1990 was relatively low, with mean

numbers of seeds/cone of 0.8 and 0.7 respectively for felled and standing treatments. The proportion of successful germinants from cones on felled stems (15 out of 22 seeds) was lower than from cones on standing trees (19 out of 20 seeds) although this difference was not significant at the 0.05 level (Chi squared = 3.30, 0.10 > P > 0.05).

H. crassifolia

The roots of one felled *H. crassifolia* plant were fully severed from the stem, while the other plant retained an almost intact root system embedded in the soil. Two follicles on the plant with the severed roots had opened by the time that the scrub-rolled strip was burnt on Day 18, with the result that the seed was incinerated inside the follicle (Fig 2). The remaining eight follicles on this stem opened within 2 hours of being burnt, and seeds were released progressively over the next 25 days. All follicles on the plant with the intact root system remained closed until after the fire and only four opened within 2 hours of being burnt (Fig 2). The remaining six follicles opened during the following 4 days, and seed was released from all but one capsule within 25 days of burning. Between March 1989 and February 1990 only 1 of the 20 follicles on the standing plants opened.

In the laboratory, the rate at which capsules opened depended on the severity of the drying regime (Fig 3). Under the most severe regime (T=35, RH=20) all follicles opened within 5 days; the intermediate regime (T=25, RH=40) resulted in 96% opening within 7 days; the solitary follicle that failed to open had been damaged by insect borers. Follicles did not begin to open until after 7 days under the mild drying regime (T=15, RH=60), and only about 70% had opened at the completion of the 27 day monitoring period. The rate of follicle opening was significantly different for each treatment (Kolmogorov-Smirnov two sample test, P < 0.01).

Discussion

Lamont (1991) has drawn attention to the need to distinguishbetween the duration of on-plant seed storage, and the mechanism of seed release. He argues that serotiny should be accepted as the technical term for canopy seed storage, and proposes a series of additional terms to describe various mechanisms of seed release. The importance of the distinction between seed storage and release

Figure 3 Rate of opening of harvested *H. crassifolia* follicles dried at three regimes of temperature (T, °C) and relative humidity (RH, %) in the laboratory: (A) T=35 RH=20, (B) T=25 RH=40, and (C) T=15 RH=60. Each treatment group consisted of 23 mature follicles.

mechanisms is clearly evident in the case of *H. crassifolia* and *B. baxteri*. Both species accumulate canopy-stored seed and can be regarded as serotinous; however differences in seed release characteristics could potentially result in scrub-rolling and fire treatments having quite different impacts on the population of each species.

Fire appears necessary to ensure synchronous follicle opening on *B. baxteri* cones, although a small proportion of follicles will open in the absence of such stimulus. Undisturbed plants exhibited low levels of follicle opening (6%) over the eleven month period of the study, and felling alone did not significantly increase the extent of follicle opening, despite the progressive desiccation of the felled stems. Witkowski *et al.* (1991) have studied seed bank dynamics in a population of *B. baxteri* near the coastal settlement of Hopetoun, some 180 km further to the east. They reported that on undisturbed plants the proportion of open follicles ranged from about 3% on 1-year-old cones to 6% on 8-year-old cones; burning stimulated more than 90% of follicles to open. They also reported that 28% of follicles opened on unburnt cones harvested and placed on the ground, a somewhat larger proportion than the 21% observed for scrub-rolled plants in this study.

In contrast, opening of *H. crassifolia* follicles was not dependent on fire *per se*, but rather on desiccation resulting from death of the plant, or severing of the follicle from the stem. This was clearly illustrated in the laboratory study where the rate of follicle opening was directly related to the severity of the drying regime. Additional evidence of the dependence on dessication can be found in the field study where follicle opening was delayed for the stem with the incompletely severed roots. Lamont (1991) has proposed the term necriscence to describe the phenomenon of seed release following the death of the seed enclosure, as exhibited by *H. crassifolia*.

Serotiny is a common trait in the genus *Banksia* with 76% of species regarded as serotinous (George 1981). Cowling & Lamont (1985a) examined populations of three *Banksia* species along a climatic gradient which extended 500 km north from Perth on the northern sandplain, and concluded that the degree of serotiny was related to the environmental characteristics of the sites where each occurred; strongly serotinous species were most common in scrub-heath communities on xeric sites. However, Witkowski *et al.* (1991) found that the degree of serotiny of *B. baxteri* and *B. speciosa* on the southern sandplain was high compared with non-sprouting *Banksia* species from the northern sandplain, and concluded that serotiny was not necessarily greater in the drier northern region. The overall extent of canopy seed storage for plant communities in south-western Australia has been found to be negatively correlated with annual rainfall (Bellairs & Bell 1990).

Fire is a characteristic feature of the southern sandplain environment due to the protracted summer drought and the high incidence of lightning strikes (McCaw *et al.* 1992). Serotiny has been interpreted as an adaptation to periodic disturbance by intense, stand replacement fires. Synchronous release of a large store of seed from the canopy may be advantageous because favourable seed bed conditions can be fully exploited (Enright & Lamont 1989b), and seed predators may be satiated by the abundant quantities available (O'Dowd & Gill 1984). Witkowski *et al.* (1991) have proposed several explanations for the co-existence of populations of weakly serotinous species such as *B. coccinea* with strongly serotinous species such as *B. baxteri*: recruitment of seedlings of the weakly serotinous species could be significant in the interval between fires; alternatively, fires could co-incide with the period of peak seed production by *B. coccinea* (age 16 to 20 years) prior to decline of the population.
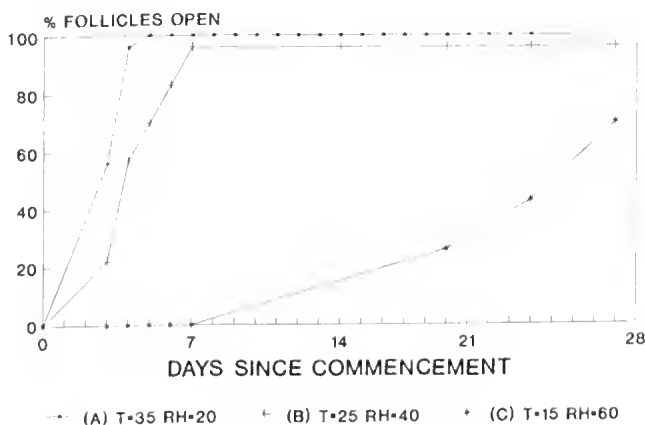
Management Implications

Where fuel-reduced buffer strips are to be established in plant communities containing *B. baxteri* and *H. crassifolia*, or a combination of other species with equivalent seed release characteristics, potential seed losses will be minimised by burning within a few weeks of scrub-rolling. The results of the laboratory study provide an indication of the rate of follicle opening expected for *H. crassifolia* under different drying conditions; factors that may tend to delay follicle opening in the field situation include diurnal variation in temperature and relative humidity, and the continued attachment of seed capsules to felled stems retaining an intact or only partially-severed root system. Weather conditions in the period following scrub-rolling will clearly have an important influence on the rate of follicle opening. Late autumn and early winter conditions are generally favourable for seed release (Cowling & Lamont 1985b) and germination (Bell *et al.* 1987, Enright & Lamont 1989b) by a range of species. Scrub-rolling operations would therefore best be scheduled in early autumn so that seed capsules on felled stems are not exposed to prolonged drying at high temperatures during the summer.

The results of this study further emphasise the important role of fire in stimulating follicle rupture in strongly serotinous *Banksia* species. Scrub-rolled areas containing a significant component of such species will require burning in order to ensure seed release is sufficient to ensure regeneration. For similar reasons, burning may also be appropriate in *Banksia* stands where a high proportion of plants have been killed by disease or insect attack. Management of degraded native plant communities is potentially an issue of profound importance in south-western Australia due to the impact of fungal diseases, particularly those caused by soil-borne species of *Phytophthora* and air-borne canker organisms. A number of serotinous *Banksia* species occur in plant communities threatened or currently seriously affected by disease.

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Geology and structural setting of ultramafic lamprophyres from Bulljah Pool, central Western Australia

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Abstract

A group of at least four ultramafic lamprophyres occur in the vicinity of Bulljah Pool, central Western Australia. These include a large sill, 1 and 2.5 ha pipes, and a 0.5 ha body of uncertain geometry. Ultramafic lamprophyres of Late Proterozoic age have previously been found in the Norseman area about 700 km to the south. The rocks at Bulljah have been dated at 305 ±4 Ma. The occurrences extend the geographic and temporal range of ultramafic lamprophyres on the Yilgarn craton. The Bulljah ultramafic lamprophyres intrude Early Proterozoic Nabberu Basin sedimentary rocks which are thought to overlie Archaean rocks of the Yilgarn craton. The bodies lie close to edge of the craton. At least one body is emplaced into a prominent tension fracture related to folding of the platform cover. Other bodies may occupy a re-activated basement shear that has been propagated through cover. Nonetheless, the host structures are unremarkable when judged in their regional context. In common with rocks of deep mantle origin elsewhere the evidence for major and unique deep seated structural control is absent or unconvincing. Like Early Proterozoic post-cratonization mafic and ultramafic dykes, younger alkaline ultramafic bodies of lamprophyric affinity appear to occupy tensional fractures in the Yilgarn craton.

Introduction

Ultramafic rocks of lamprophyric affinity and Late Proterozoic age (849 ±9 Ma, Rb-Sr mica) have previously been reported by Robey *et al.* (1986) near the southeastern margin of the Yilgarn craton (Fig 1).

A discovery of ultramafic lamprophyres (UMLs) near Bulljah Pool, central Western Australia (Fig 2) was made in March 1986 by Western Mining Corporation Ltd (Hamilton 1988). The discoveries followed from the recognition of kimberlitic indicator minerals in drainage samples in May 1985.

Four bodies were found. Sampling results suggest that a larger number of very small bodies also may exist. This paper provides details of the geology and structural setting of the Bulljah lamprophyres and compliments an account of their petrology (Hamilton & Rock 1990).

Regional Setting

The area under consideration lies within the Earaheedy Sub-Basin, which forms the eastern limb of the Early Proterozoic Nabberu Basin (Fig 1). The UMLs intrude a gently dipping, relatively undisturbed part of the Earaheedy Sub-Basin, the Kingston Platform. The area is underlain by the Archaean Yilgarn craton. The lamprophyre bodies appear to lie close to the northern edge of the craton.

The structural province to the north of the area of interest is the Stanley Fold Belt. This belt of folded rocks is equated with a failed rift, the Capricorn Orogen (Bunting & Grey 1986). The northern boundary of the Capricorn Orogen is the Archaean Pilbara craton. Thus the setting is marginal to a major orogen dividing the two cratons of the West Australian Shield.
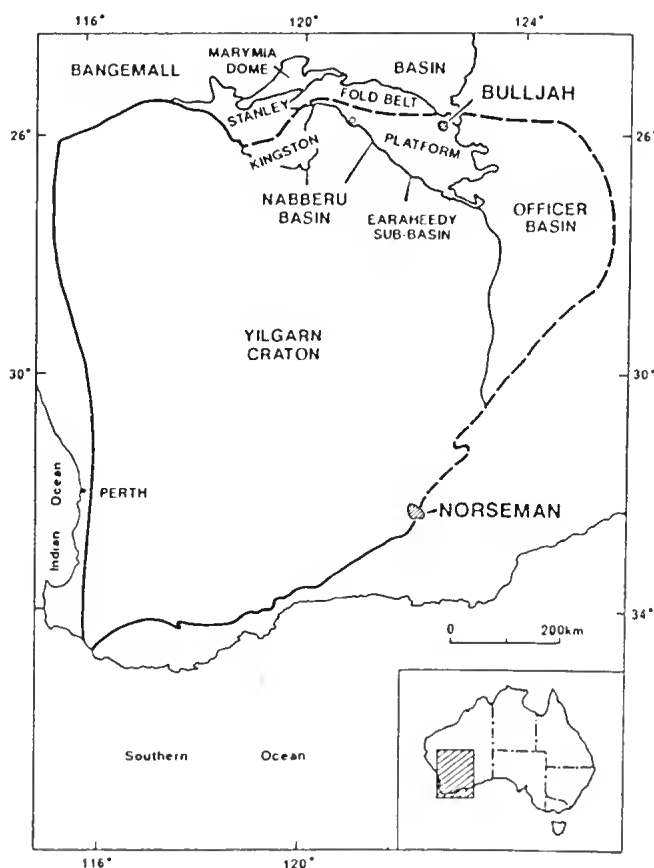
Figure 1 Regional tectonic setting of ultramafic lamprophyres in southern Western Australia. Occurrences at Bulljah and Norseman are hatched. The edge of the Yilgarn craton is shown as a heavy line or where inferred, by a broken line.
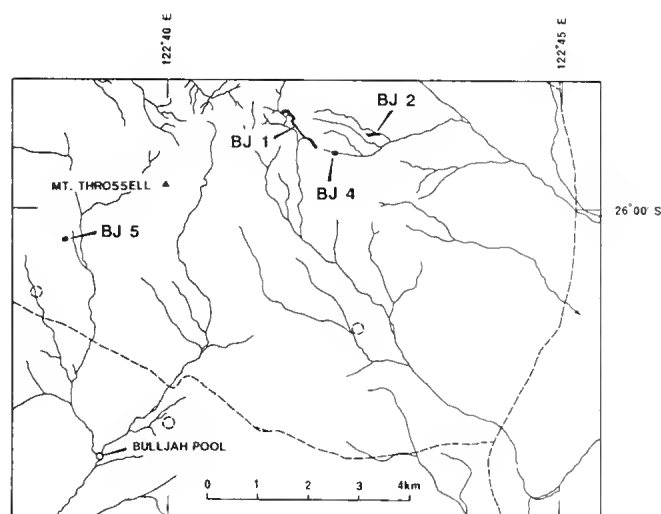
Figure 2 Locations of alkaline ultramafic rocks. The dashed circles are areas where the presence of small bodies is suggested by soil indicator mineral anomaly spreads. Broken lines are tracks.

Depth estimates to magnetic basement indicate that the platform cover in the study area is about 2.3 km thick. Dolerite dykes and sills are common in the Bulljah area and have the general orientations 0° and 315° respectively. A dolerite in the Earaheedy Group about 100 km southeast of Bulljah Pool, yielded a Rb-Sr date of 1028 ±50 Ma (recalculated after Compston 1974). The enigmatic Teague Ring Structure which is cored by *ca.* 1630 Ma quartz syenite is located about 180 km to the west within the Earaheedy Group (Bunting *et al.* 1980). No other magmatic rocks have previously been reported from the basin.

Age of the Bulljah Rocks

A selection of zircon grains from concentrates from the body BJ5 were analysed by the ionprobe U-Pb method. The youngest zircon age obtained was 305 ±4 Ma (Compston 1986). This Carboniferous age is taken to be the age of crystallisation of the BJ5 body.

Geology of the Bulljah Rocks

Four bodies have been discovered and investigated in various detail. The presence of at least another four small bodies may be inferred from detailed drainage sampling (Fig 2). The known bodies are pipes (BJ2, BJ5), a sill (BJ1) and an outcrop of unknown geometry (BJ4). A feature originally termed BJ3 was found to be non-lamprophyric. Wall rocks to the bodies are fine to medium grained sandstones and calcarenites. The bodies are contained within the area of a 14 km diameter circle.

Although they are deeply weathered, the original modal constituents have been shown to be phlogopite, olivine, diopside, calcite and perovskite with accessory spinel. Mineralogical and petrographic details are provided by Hamilton & Rock (1990) and Archer (1987). The mineralogy and geochemistry indicates that the rocks are ultramafic lamprophyres with affinities to classical kimberlite.

Sill BJ1

This large sill outcrops discontinuously along the face of a northwest trending scarp for a distance of over 1,000 m. The body is about 20 m thick and dips shallowly to the northeast (Fig 3a).

Weathered outcrops show textures reminiscent of an olivine-phyric, phlogopite-rich ultramafic rock. Petrographic examination supports this identification. Altered perovskite is abundant in all outcrops (4-6 percent by weight).

A concentrate from a surface exposure contained abundant perovskite and spinel, a number of almandine-rich
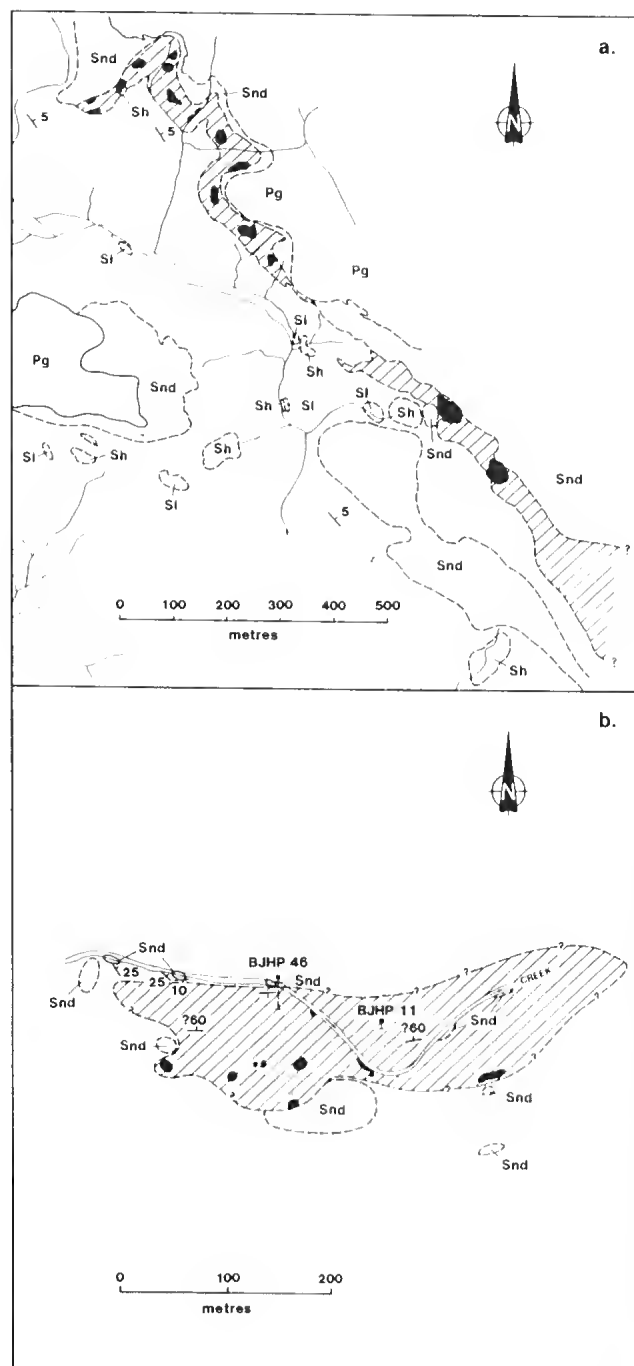
Figure 3 Geological maps of BJ1 and BJ2. **a.** BJ1. The sill (hatched) is intruded between the Early Proterozoic Kulele Limestone and Mulgarra Sandstone (Snd): outcropping lamprophyre is black. Paterson Formation Sh, Sl, glacial sediments are Pg; **b.** BJ2. This pipe-like body (hatched) is intruded into Mulgarra Sandstone. Legend as for **a.**

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garnets and a single 0.25 mm microdiamond. Although the diamond was not confirmed by subsequent sampling it was believed to be genuine. The rare presence of diamond in the sill BJ1 may therefore be inferred.

Pipe BJ2

This is a steeply dipping, 2.5 ha lens-like body which is aligned east-west. A small exposure of xenolith-rich material in a stream bank marks the discovery location (Fig 3b). The body lies on the southern edge of an intense conductivity anomaly which coincides with a strong 285° trending linear feature. Sandstone outcrops within this zone are sheared at 285° silicified and dip steeply to the north.

Enclosing sandstones have been fenitized. The body itself contains lenses of recrystallised sandstone, abundant xenoliths of country rock sandstone and zones of magmatic material.

Materials obtained from drill holes reveal a tetriferriphlogopite, diopside, titanomagnetite, olivine, perovskite mineralogy. Surface concentrates contain rare chrome diopside, andradite and a little diopside, phlogopite and chromite.

Outcrop BJ4

This small outcrop occurs on the northern dip slope of the range of hills hosting the BJ1 occurrence.

Weathered textures suggest an olivine-rich ultramafic rock. Concentrates contain umerous chromites, a range of almandine-rich garnet, and rare chrome pyrope. The absence of perovskite in both loam and thin section samples is evidence that this body is not part of the BJ1 sill. Diamond was not recorded from this locality.

Pipe 5

Close spaced trenching revealed that this body has an area of one hectare. It is sparsely vegetated compared with surrounding flatly-dipping units of the ca. 1.6 Ma Kuluele Limestone. Weathered rock extends to within 50 cm of the ground surface.

Pipe 5 was the most extensively explored of the Bulljah UMLs (Fig 4a). It lies within a well defined 11 ha conductivity anomaly which trends at 305° (Fig 4b).

The conductivity anomaly is interpreted as a steep northeasterly-dipping shear structure. Pipe 5 appears to have been emplaced at the point of intersection of this structure and a vertical north-south fracture system. A concealed dolerite dyke occupies a central position in the north-south fracture.

A 1 ha zoned body (magmatic and tuff facies) was interpreted from magnetic field data (Fig 4a) and very weathered materials in trenches. Drill evidence however suggested that body number 5 is made up of a number of small dykes contained within a steep northeasterly dipping (tectonic) breccia pipe. In this interpretation short 305° striking dykes with the same plunge as the breccia pipe are interlayered with hornfelsed country rock calcarenites and occupy "jog" type tensional partings in the breccia pipe.

Concentrates yield numerous grains of low-calcium chrome pyrope, chrome pyrope, almandine-rich garnet, chrome diopside, apatite, barite, phlogopite, andradite-melanite, pargasite and iron and chromian spinels. Trace amounts of perovskite, picroilmenite, rutile and zircon are present.

A diversity of magmatic and xenolith-rich lamprophyre facies is revealed in drill cores. Pipe 5 is essentially a tetriferriphlogopite, olivine, calcite, diopside rock with variable country rock xenolith dilution. Spinel lherzolite nodules up to about 5 cm in size were found in drill core.
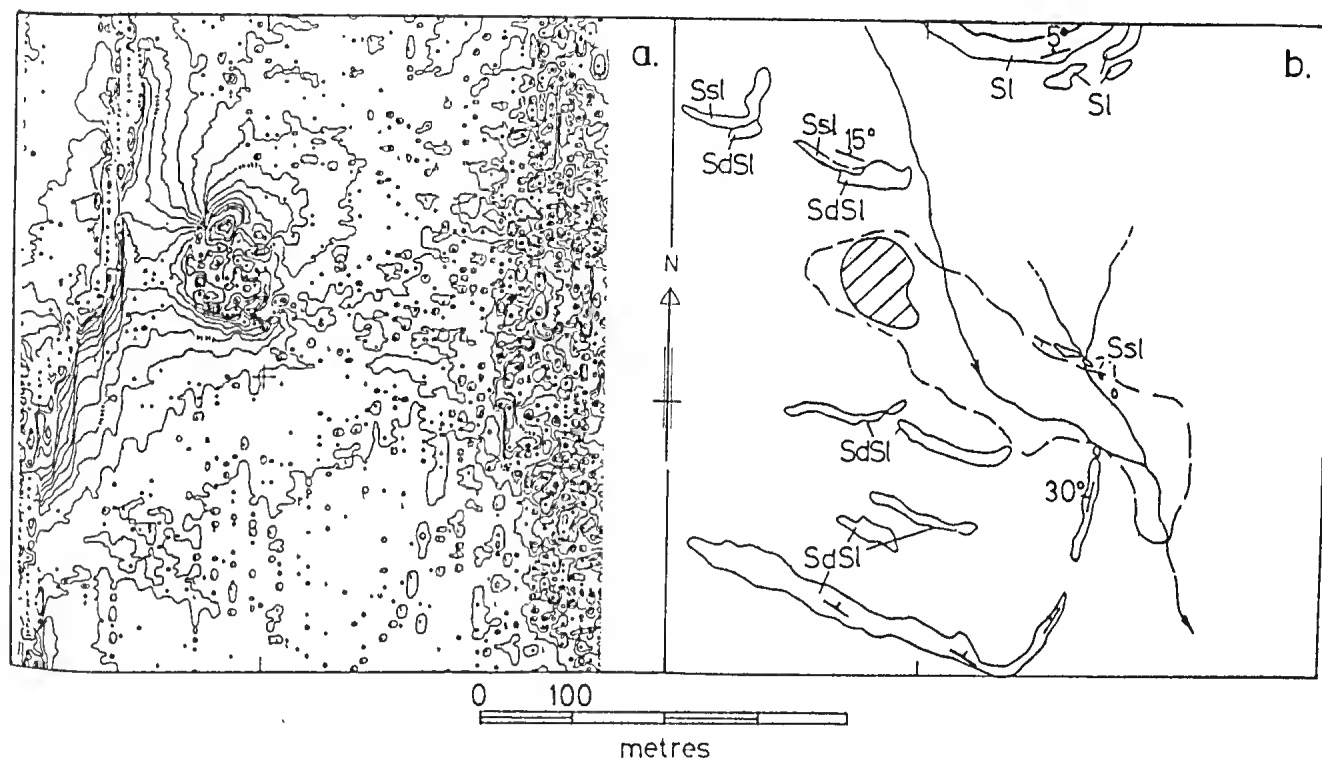
Figure 4 Details of body BJ5 **a.** Detailed ground magnetometer survey. Lines 10 m apart, sampling 1 m intervals. The linear western anomaly is due to unexposed dolerite, the eastern noise band coincides with a palaeochannel; **b.** Simplified geological map. The body is hatched and intrudes ca. 1600 Ma Kulele Limestone: the following lithologies are present: SdSl, stromatolitic limestone; Sl, calcarenite; and Ssl, siltstone. The broken line is a conductivity anomaly.
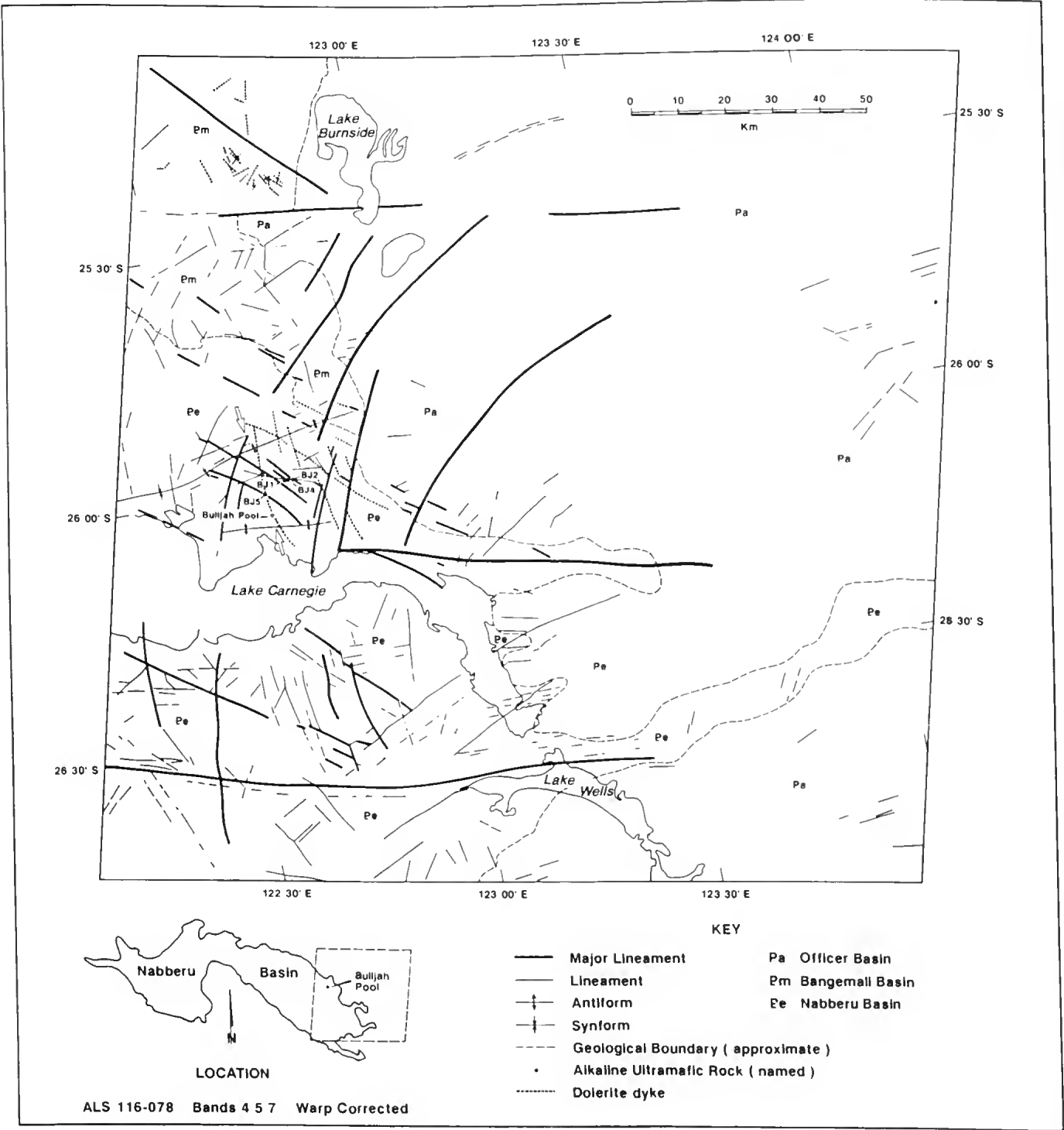
Figure 5 Lineaments in the eastern part of the Earaheedy Sub-basin and surrounding areas from a Landsat(TM)-based interpretation. Geology simplified from Bunting (1980), supplemented by Western Mining Corporation mapping in the Bulljah Pool area.

Other Localities

The presence of other small bodies was strongly suspected from indicator mineral stream sediment sampling. The localities of these bodies are shown in Fig 2.

Structural Setting of the Bulljah Field

A regional synclinorium extends throughout the Kingston Platform. The axial trace of this structure is shown on the Landsat-based lineament map (Fig 5). The prominent curved linear features are interpreted to be wrench faults associated with compression and regional folding. Dolerites of presumed Late Proterozoic age utilise related tensional partings in the Bulljah area.

The BJ5 body lies 100m east of the intersection of a major northerly striking dolerite-filled fracture and a northwesterly striking conductivity anomaly which has been interpreted as a shear zone (Fig 4). Both these features are visible on Landsat images (Fig 5).

A prominent 285° lineament is visible both on Landsat and on the ground and is associated with BJ2 and possibly BJ1 and BJ4 (Fig 5). This structure is incompatible with the previously described cover structures. Basement rocks presumably folded in the Late Archaean, appear from Bureau of Mineral Resources gravity and magnetic maps to trend at 325°. Tensional shears orientated at about 290° are predicted to arise from this deformation. The linear BJ2 is one of a number of 290° trending lineaments (Fig 5). The 290° linear features may result from the re-activation and propagation through cover of major basement shears.

Conclusions

A new, hitherto unrecognised, region of alkaline ultramafic rocks has been identified. The two known localities are confined to the opposite extremities of the eastern half of the Yilgarn craton (Fig 1). It is perhaps significant that these rocks are found in a part of the craton which is characterised by a wide north-south aligned band of mildly alkalic rocks of diverse ages (Libby *et al.* 1978). Rock (1988) suggests that calc-alkaline lamprophyres may be widespread on the Yilgarn craton. As this is one of only a few known occurrences of ultramafic lamprophyre these rocks appear to be relatively uncommon.

High level host structures at Bulljah may be ancient tensional features of both Archaean and Proterozoic age which have been re-activated, perhaps in Carboniferous time, and in the case of the Archaean shear, propagated through cover. Similar though apparently lamprophyre-free structures are common in this part of the Nabberu Basin. The location of the Bulljah Field near the northern, presumably structurally bounded edge of the Yilgarn craton may be significant. Ultramafic magmas of this type may be generated in the asthenosphere. Their ascent may require that a fracture or system of fractures be present throughout the entire thickness of the continental plate. It seems remarkable that here as nearly everywhere else where rocks of deep mantle origin are found, evidence for major and unique structural control is either absent or unconvincing.

Post-cratonization mafic and ultramafic dykes utilise tensional fractures in the Yilgarn craton (Hallberg 1987). Widespread and rare intrusion of ultramafic lamprophyres may have been the most recent magmatic event to effect the craton.

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The reproductive cycles of a number of species of lizards from southern and north-western regions of Western Australia

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Abstract

Routine histological examination of the gonads of a number of species of reptiles, collected primarily in Western Australia over a period of more than a decade, enables a number of general conclusions to be drawn concerning their mode of reproduction in relation to climate and their geographical distribution.

In the south-western region of Western Australia, characterised by a typical mediterranean climate with wet winters, spermatogenesis is prenuptial and breeding typically vernal. In mediterranean arid regions (such as Shark Bay) most of the small polyoestrous oviparous species display precocious vernal breeding, whereas monoestrous species breed also in spring, but late rather than early.

In arid subtropical regions of Western Australia (such as the Pilbara) where rainfall is primarily confined to the summer months, reproduction tends to be either aestival or autumnal. Co-existing species can be found however displaying quite different patterns of reproduction. Polyoestrous oviparous species (such as *Amphibolurus nuchalis*) show a propensity for continuous extended breeding, from spring to late summer, depending upon the available resources which appear to be a function of the local climatic conditions in any one year.

The data presented reinforce the conclusion that, in arid regions where resource availability may be particularly aleatory, many reptilian species adopt an opportunistic approach to reproduction which may lead to large differences in the timing of breeding from year to year.

Introduction

Reproductive cycles in lizards are quite diverse, varying both as a function of the systematic position of the species concerned, as well as the climatic conditions to which it is exposed (see reviews by Fitch 1970, 1982, Fox 1977, Duvall *et al*. 1982, Saint Girons 1985, Craig & Shine 1985). Although there is now considerable information available on the reproductive patterns of species inhabiting temperate and arid mediterranean regions of the northern hemisphere and, to a lesser extent, species from humid sub and intertropical zones, we know little of species occupying intermediate biotopes, especially in Australia (Shine 1985) and particularly concerning the cycle of males. It therefore appeared pertinent to assemble the various data that we have acquired over a period of years concerning states of reproduction of a number of species of lizards from Western Australia. This vast State spans 21° of latitude (14°S to 35°S) and almost 14° of longitude and shows considerable climatic variation, ranging from typical temperate mediterranean in the south-west, characterised by regular winter rains and hot dry summers, to arid sub-tropical regions in the north-west of the state where rainfall comes primarily from summer cyclones (see Bradshaw 1986 for more details).

Unfortunately, our data are not homogeneous, as they have often been collected as an annexe to other studies of the ecophysiology of these lizards, but a coherent pattern does emerge, particularly when cognizance is taken of the results of more detailed local studies already reported (see Bradshaw 1981, Saint Girons & Bradshaw 1981, Mendonça *et al*. 1990, Bradshaw *et al*. 1990).

Materials and Methods

Lizards were primarily collected between 1976 and 1988 (with a few specimens going back as far as 1963), either close to Perth (31°50'S, 116°E) which has a temperate mediterranean climate with hot dry summers; or at Shark Bay (26°S, 114°E) where the climate is still mediterranean, but very arid, with an average of only 212 mm of rain, 67% of which falls in the winter months (May-August); or in the arid north-west Pilbara region of the State, primarily on Mallina Station (21°S, 118°E) where the climate is arid sub-tropical with an average annual rainfall of 370 mm, 75-80% of which falls in the summer months. Data from 16 species of lizards are reported (see Table 1 for details) and individuals were first bled by cardiac puncture and then killed with an overdose of sodium pentobarbitone and the testes, epididymis, kidneys and vas deferens removed from males and the ovaries and, occasionally, the oviducts removed from females. Plasma was separated from the blood by centrifugation at 1500 *g* and then stored frozen at -20°C until assayed for hormonal levels.

Tissues were fixed under negative pressure in Bouin's, with a change of fluid after 24 hr, dehydrated, and then embedded in paraffin and cut at 5 μm. Sections were stained with PAS-haematoxylin-picro-indigocarmine, haematoxylin and eosin, single trichrome and/or Gabe's azan. Criteria of sexual activity noted and/or measured on each slide were: the mean diameter of the seminiferous tubules and the state of the seminiferous epithelium; the maximal height of the epididymal epithelium; the diameter of the middle section of the sexual segment of the kidney and the serous or mucous state of its epithelium, and the abundance of spermatozoa in the epididymis and vas deferens. Stage of spermatogenesis was classified from 1 (regressed) to 7 (spermiation) following the schema of Licht

(1967) and Marion (1982). These schemes however do not generally take account of associated histological changes in the sexual segment of the kidney, which normally hypertrophies and becomes serous by the end of Stage 4, or the beginning of Stage 5, and regresses at the end of Stage 7 in those lizards with prenuptial spermatogenesis. Nevertheless, in some instances, it was not possible to assign the testicular state to any of the above categories and these have been classified as A (abnormal) and are described in the text. In the case of females, the diameter of the largest follicle in the ovaries was measured, and *corpora lutea* noted and counted, and the oviducts were examined for the presence of eggs.

Circulating levels of sex steroids were measured in the plasma of a number of individuals of the various species that were studied histologically, enabling correlations to be made. Concentrations of progesterone (P), oestradiol-17β (E2), testosterone (T) and 5α-dihydrotestosterone (DHT) were measured by radioimmunoassay in 50 μl samples following the procedures detailed by Bradshaw *et al.* 1988. All statistical tests on the difference between mean values were by Student's "t" test.

Results

Reproductive status of collected specimens

1. Amphibolurus (=Ctenophorus) nuchalis

The reproductive cycle of this annual species has already been described in some detail (see Bradshaw 1981, Bradshaw *et al.* 1990) and will only be briefly resumed here. At Shark Bay, this lizard breeds regularly in spring and by October-November all individuals show evidence of maximal sexual activity. Females generally lay two clutches and, occasionally, a third in early summer. By March, the rare survivors in the population are normally completely sexually regressed, although some males may give evidence of an evanescent spermatogenic activity.

The reproductive cycle of more northern populations of this species, occurring between Cape Range and Port Hedland (20°-23°S), is much more variable. In years when winter rainfall is adequate, reproduction occurs in spring (October-November) and may continue right up until March or April if supported by summer rains. In years with particularly dry winters, however, reproduction is deferred until January or February to coincide with the cyclonic rains characteristic of this region. In such years, spermatogenesis commences in spring, but remains abnormal and the testicular volume remains small. Even though some spermatozoïds are produced, the secondary sexual characters remain involuted and, in females, some vitellogenesis may occur but this never proceeds to the point of ovulation. When reproduction is retarded in this way, adult survival throughout the summer period is high with most mortality occurring in late autumn whereas, following spring breeding, summer mortality of adults is significant.

2. Amphibolurus caudicinctus

The reproductive cycle of this species in the Pilbara is as regular as that of *A. nuchalis* at Shark Bay, but virtually the inverse in terms of actual detail. In March 1984, 1986 and 1987, the 5 males were at the peak of their sexual activity and the 20 females studied all had pre-ovulatory follicles, or eggs in the oviducts. By May 3 in 1985, however, reproduction was terminated and the 9 males collected all showed signs of testicular regression and involution of secondary sexual characters. The ovaries of the 3 females collected contained only small translucent follicles and numerous *corpora lutea* aged between 4-6 weeks. In September-October of 1978 and 1986, the 6 males and the 4 females

autopsied were all regressed. In December 1985 and January 1986, Mendonça *et al.* (1990) autopsied 7 males and found they were either still regressed or just commencing spermatogenesis. Bradshaw (1981) found, from an examination of preserved museum specimens, that vitellogenesis commences in January in this species with eggs being laid in February and March. The cycle is thus extremely regular, with a short period of breeding in late summer or early autumn, following the regular cyclonic rains that are characteristic of the Pilbara region of north-west Western Australia.

3. Amphibolurus isolepis

All except one specimen of this species were collected on Mallina Station in the Pilbara. Five males collected in November 1984, 1986 and 1987 were in various stages of early spermatogenesis (Stages 2-3) and one male collected on December 6 in 1987 had reached Stage 4. Six females collected in November 1984 and 1985 were sexually regressed; however, one male collected on October 21 in 1978 at Wittenoom, in the Pilbara, (22°30'S, 118°30'E) was already capable of breeding. On March 28 in 1984, one male was in full sexual activity and two of the three females autopsied at that time had large pre-ovulatory follicles in the ovaries. In May 1985, five females autopsied all had completely regressed gonads. *A. isolepis* thus appears to have an essentially aestival pattern of reproduction, with breeding being concentrated in the period from January to March or April, and with spermatogenesis commencing in spring.

4. Amphibolurus (=Pogona) mitchelli

One male was collected on Mallina Station in full sexual activity on March 1 in 1986 and another on December 7 in 1987, along with 3 females with oviducal eggs in November 1986. All the females collected in November 1984 were, however, regressed which suggests that this species has a reproductive cycle similar to that of the northern populations of *A. nuchalis*: breeding in spring when resources are adequate, but deferring reproduction until late summer or autumn in drier years.

5. Other Agamids

In *Amphibolurus (=Pogona) minor* and *A. (=Ctenophorus) clayi*, the two males were at the height of their sexual activity in October 1978. In the case of the former species, it is known that females lay their eggs in August and September in regions north of latitude 30°S (Bradshaw 1965, 1981), indicating a very precocious vernal cycle of reproduction. *A. clayi* may show a similar cycle but the data available for this species are too few to exclude the possibility that reproduction is prolonged until the summer period.

The one male *Diporophora bilineata* autopsied was in full breeding condition in March 1986, suggesting a pattern similar to that of *A. caudicinctus* which breeds in late summer and autumn following the cyclonic rains. Given the northerly distribution of *D. bilineata* in Australia, this seems a logical conclusion but, again, the data do not exclude the possibility of "deferred reproduction" as the winter of 1985 was particularly dry in the Pilbara and species such as *A. nuchalis* did not breed in the spring of that year (Bradshaw *et al.* 1991).

One male *Lophognathus (=Gemmatophora) longirostris* collected on Mallina Station was in full breeding condition in November 1986, and another collected in September 1963 in Alice Springs in central Australia, was at an early stage of sexual activity. This species thus also appears to have a precocious vernal cycle which accords with field observations of males courting females early in spring.

6. Scincidae

In the vicinity of Perth, *Tiliqua rugosa* displays a classic vernal cycle which has already been described in broad detail by Bamford (1980), Fergusson (1988), Fergusson & Bradshaw (1991) and Shea (1989). From the analysis of the 4 males autopsied immediately after their capture, the cycle in males is exceptionally brief, with spermatocytogensis occurring in September, spermiogenesis in October, and the testes have fully involuted by the end of November. The sexual segment of the kidney is only hypertrophied from about mid-October, which places actual breeding and copulation at the end of October, and extending possibly into the first two weeks of November. One female collected on November 16 in 1978 had not yet completed vitellogenesis and had spermatozoa in the oviduct. Clearly, there is only one clutch per year in this viviparous species.

A male *Egernia kingii*, collected close to Perth, was in early spermiogenesis on September 28 in 1978, suggesting a similar cycle to that of *T. rugosa*, or one which is slightly more precocious. In contrast, a male *T. occipitalis* from Shark Bay was only at Stage 2 on October 15 in 1978, and at the same time *T. brachialis* from Cape Range was still completely sexually regressed.

7. Gekkonidae

Between October 15-18 in 1978, two male *Heteronotia binoei* and *Rhynchoedura ornata* collected at Cape Range were in full breeding condition, showing that they also possess a vernal cycle. More data are required however to exclude the possibility that their cycle is similar to that of *A. nuchalis*, extending into summer, depending upon the availability of resources. *H. binoei* occurs as both bisexual diploid populations and parthenogentic triploid populations in Western Australia (Moritz 1983, 1984) and the Cape Range animals are obviously bisexual.

8. Pygopodidae

By October 15 in 1978, a male *Lialis burtonis* from Cape Range had commenced spermiogenesis (Stage 3) but the sexual segment of the kidney was still involuted and mucous. Breeding could thus not occur before the end of November, which correponds to a very late or retarded vernal cycle.

Histological modification of the testis and genital tract with breeding

The data compiled in Table 1 show clearly that the histological criteria chosen (diameter of the seminiferous tubules; height of the epididymal epithelium and diameter the of collecting ducts in the sexual segment of the kidney) vary greatly (P<0.001) when comparing samples collected in different seasons. The same is also true, although to a lesser degree, when considering *A. nuchalis* in the dry years of 1985 and 1987 on Mallina Station at Port Hedland when reproduction was 'deferred' until the following year and the stage of spermatogenesis designated 'A = abnormal': the diameter of the seminiferous tubules was significantly greater than that of regressed individuals from Shark Bay (P<0.01) but less than that of Mallina males in full breeding condition (P<0.001). The secondary sexual characters on the other hand appear to remain atrophic in 'deferred' males and this accords with the low circulating levels of testosterone recorded in these individuals (see Table 3).

As a general rule in squamates, the maximum and minimum diameters of the seminiferous tubules and the sexual segment of the kidney may differ from one Family to another, but are usually fairly characteristic within a given Family, and even more so within a single genus. This characteristic variation appears to be little influenced by the size of the animal and this facilitates meaningful inter-taxonomic comparisons (Saint Girons 1972). This is certainly the case with the West-Australian agamids studied in this paper where, for a given stage of the sexual cycle, the diameters of the seminiferous tubules and the sexual segment of the kidney are virtually identical in all species. Table 1 shows that, in fully breeding males, the Coefficient of Variation (CV) for the overall mean for the diameter of the seminiferous tubules is only 5.55% for 7 species of agamids and 7.27% for the diameter of the sexual segment of the kidney for 6 agamid species plus the skink *Tiliqua rugosa*. Data from the agamid species included in this study have been plotted in Fig 1 and they document a progressive increase in the diameter of the seminiferous tubules with increasing stages of spermatogenesis, followed by a later and somewhat more attenuated change in secondary sexual characters as reflected in the diameter of the tubules in the sexual segment of the kidney.

Hormonal correlates of reproductive activity

Data from three species, *A. mitchelli*, *A. minor* and *L. longirostris* are shown in Table 2, by date of capture, and all animals were collected on Mallina Station in the Pilbara during the period 1984-1987. Inspection of the data for *A. mitchelli* shows that levels of testosterone (T) are always significantly higher in males than in females and DHT shares the same trend, although this only reaches statistical significance in the March 1986 sample. Levels of progesterone (P) are higher in females than in males in March 1984 and 1986, but not at other times of the year. Blood samples were only collected from three males in November (one each in 1985, 1986 and 1987) but levels of T are uniformly high at 15.87±2.07 ng/ml and significantly greater than the levels measured in late summer (5.44±0.79 ng/ml, P<0.001, see also Table 3).

Plasma levels of testosterone and DHT show a significant positive correlation in *A. minor* (r=0.89, P<0.01) and the correlation is also close to significance for *A. mitchelli* (r=0.51, P=0.06). These two hormones are similarly correlated in *A. nuchalis* and *A. caudicinctus* as shown with the larger data set of Bradshaw *et al.* (1991). It is also possible to glean something of the nature of the variation in testosterone levels in males with changes in state of development of the testes and the data available are presenteed in Table 3. In *A. nuchalis*, levels of T remain low in individuals in Stages 7 and 'A', whereas with *A. caudicinctus* there is a significant increase from 10.89±1.29 to 37.32±7.7 ng/ml in passing from Stages 7-1 to Stage 2. Plasma T levels reach the maximum recorded of 59.9±20.0 ng/ml in male *A. nuchalis* in Stages 3-5 and these remain at this level up until Stage 5-6.

There are few data from *A. mitchelli* but levels of T, which generally appear lower than those in either *A. nuchalis* or *A. caudicinctus*, fall significantly from a mean of 15.9±2.1 to 5.4±0.8 ng/ml (P<0.001) from early (Stage 5) to late in reproduction (Stage 6). Testosterone levels also appear low in *A. minor*, averaging 3.3±0.9 ng/ml from 7 males in Stage 6.

Discussion

The nature of the reproductive cycle is only one of the many elements forming part of the perceived demographic strategy of any species and, in the case of lizards, the precise relationship between the sexual cycle and the climate to which the animals are habitually exposed is far from clear (see Saint Girons 1984, Craig & Shine 1985, Bradshaw 1986). The only factor to emerge consistently in the case of species occupying cool temperate regions is that embryonic development is restricted to, and must be completed during the warm season of the year.

Table 1

State of the male gonad, genital tract and sexual segment of the kidney in West-Australian lizards from different habitats (data presented as mean±SE with number of individuals in parentheses). The statistical significance of differences between means within columns is indicated by the P value inserted between the two means concerned.

Species, Date & Origin[1]	Geographic[2] distribution	Stage of[3] spermato- genesis	Diameter of seminiferous tubules (μm)	Height of epididymal epithelium (μm)	Abundance of sperm in vas deferens	Sexual Segment of kidney	
						Diameter of tubules (μm)	Nature
Amphibolurus nuchalis Sept-Oct '76, '77 Shark Bay	CNW	6	253±13.65(5) P<0.001	45.0±1.6(5) P<0.001	+++	106.4±5.2(5) P<0.01	Serous (S)
March '77, '83 Shark Bay		1	118.8±7.1(6) P<0.01	23.0±0.5(2) NS	+++	51.5±1.5(2) NS	Mucous (M)
Nov-Dec '85, '87 Port Hedland			157.6±5.9(17) P<0.001	28.3±1.5(6) P<0.001	0++	60.4±3.5(6) P<0.001	M
Oct-Nov '78, '84, '86, Feb '86 Port Hedland		5-6	216.2±13.5(11) NS	45.7±1.7(7) P<0.01	+++	101.8±7.0(5) NS	S
Mar '84, '87 May '85 Port Hedland		6.5-7	197.6±15.9(8)	34.4±3.6(5)	+++	70.5±17.5(2)	SM-M
19 Aug '63 Alice Springs		6	275	55.0	+++	110	S
20 Aug '63 Alice Springs		4-5	193.5±6.5(2)	42.5±2.5(2)	±	72.5±2.5(2)	SM
Amphibolurus caudicinctus Sept-Oct '78, ''86 Port Hedland	NW	1	90.4±5.1(6) P<0.001	12.5	0	42.5	M
Mar '84, '86, '87 Port Hedland		5-6	218.1±8.3(5) P<0.001	47.5±1.3(4) P<0.001	+++	92.5±2.5(2) P<0.01	S
May '85 Port Hedland		1-7	71.1±6.3(9)	17.5±1.7(7)	0++	59.4±4.4(9)	S-M
Amphibolurus isolepis 21 Oct '78 Port Hedland	CNW	4-5	150	35.0	++		
Oct-Nov '84, '86 Port Hedland		1.5-3.5	87.5±12.1(4)	23.7±5.1(3)	0		
27 Nov '87 Port Hedland		3	113.0	22.5	+	45.0	M
6 Dec '87 Port Hedland		4	189.0	35.0	+	80.0	S
Mar '84 Port Hedland		6	240.0	47.5	+++	110.0	S
Amphibolurus mitchelli 7 Dec '87 Port Hedland	NW	5	240	55.0	+++	105	S
8 Mar '86 Port Hedland		6	237	57.5	+++	120	S
Amphibolurus clayi Oct '78 Cape Range	NW	6	220.0		+++	100	S
Amphibolurus minor Oct '78 Cape Range	CNW	6	220.0		+++	95	S
Diporophora bilineata Mar '86	NW	6	187.5	50.0	+++		
Lophognateus longirostris 21 Aug '63 Alice Springs		4	162	30.0	0	60	M
Nov '86 Port Hedland		6	212.0	35.0	+++		
Tiliqua rugosa 2 Oct '78 Perth	SW	3-4	209.5±9.4(2) P=0.004	44.5±10.5(2) P=0.03	0	62.5±17.5(2) P=0.05	M-S
19 Nov '78 Perth		7	147.0±9.0(2)	76.3±1.3(2)	+++	102.5±2.5(2)	S
Egernia kingii 28 Sept '78 Perth	SW	4	225		0		
Tiliqua occipitalis 15 Oct '78 Shark Bay		2	90		0		
Tiliqua brachialis 15 Oct '78 Cape Range		1	80	12.5	0		
Heteronotia binoeix 15 Oct '78 Cape Range	CNW	6	200	48.0	+++	155	S
Rhyncoedura ornata 18 Oct '78 Cape Range		6	175	35.0	+++		
Lialis burtonis 15 Oct '78 Cape Range	A	3	130		0	55	M

[1]Following taxonomy of Cogger H (1979) but see also Storr G M (1988) Records of the Western Australian Museum 10:199-214.

[2]CNW = Central deserts to North West Pilbara region
NW = Sub-tropical arid North West of Australia
SW = Temperate south west of Australia
A = all Australia

[3]According to Licht (1967) and Marion (1982).

All of the lizards studied here show prenuptial spermatogenesis which means that, in the vicinity of Perth where winters are still relatively cool, precocious vernal reproduction is excluded. Effectively, copulation cannot occur before the end of October but the breeding season may be longer in poly-oestrous oviparous species such as *A. ornatus* than in mono-oestrous viviparous species such as the skinks *Tiliqua rugosa* and *Egernia kingii*.

Further north, in the region of Shark Bay, where the climate is still of mediterranean type but much hotter and more arid, desert species can be found co-existing with temperate species that are here at the northern limit of their distribution. Amongst the former, *A. nuchalis* and *L. longirostris* show precocious vernal reproduction, laying eggs from September-October until December-January and thus with spermatogenesis commencing in July or August. In contrast, if one judges by the stage of spermatogenesis reached by mid-October, *T. occipitalis*, a species of temperate origin, breeds later at Shark Bay than the other two large skinks do in the region of Perth - even though the geographic distribution of the three species is broadly similar.

The lizards studied in the region between Cape Range and Port Hedland, where the climate is arid subtropical with summer rainfall, display a diversity of patterns. Amongst these desert species, *A. nuchalis* and probably *A.*

mitchelli show a proclivity to breed continuously from September until March, if resources are adequate to sustain their reproductive effort. This is because the Pilbara region of Western Australia, although essentially a summer rainfall area, also receives, on average, a not insubstantial winter rainfall (an average of 87 mm for example was recorded during the winter months on Mallina Station over the period 1900-1926, and 99 mm between 1952-1985) which is sufficient to stimulate spring breeding in these species. If cyclonic rains then follow in January and February, as is usually the case, these species may thus prolong their breeding season for a period of approximately six months before the adults die at the end of summer (see Bradshaw *et al.* 1991). In years when winters are particularly dry however (such as in 1983, 1985 and 1987 during the present study), these species show evidence of poor condition in spring and defer their reproduction until the summer months, following the regular cyclonic rains. These species thus appear to be opportunistic, resource-limited, but essentially vernal breeders, which are dependent upon precipitation-driven insect abundance to fuel their reproduction.

A. isolepis on Mallina Station appears to be an aestival breeder, whereas *A. clayi* and *Rhyncoedura ornata* are clearly spring breeders, although it is not known whether, in dry years, they prolong their breeding into summer. Aestival spermatogenesis with egg laying in February and March
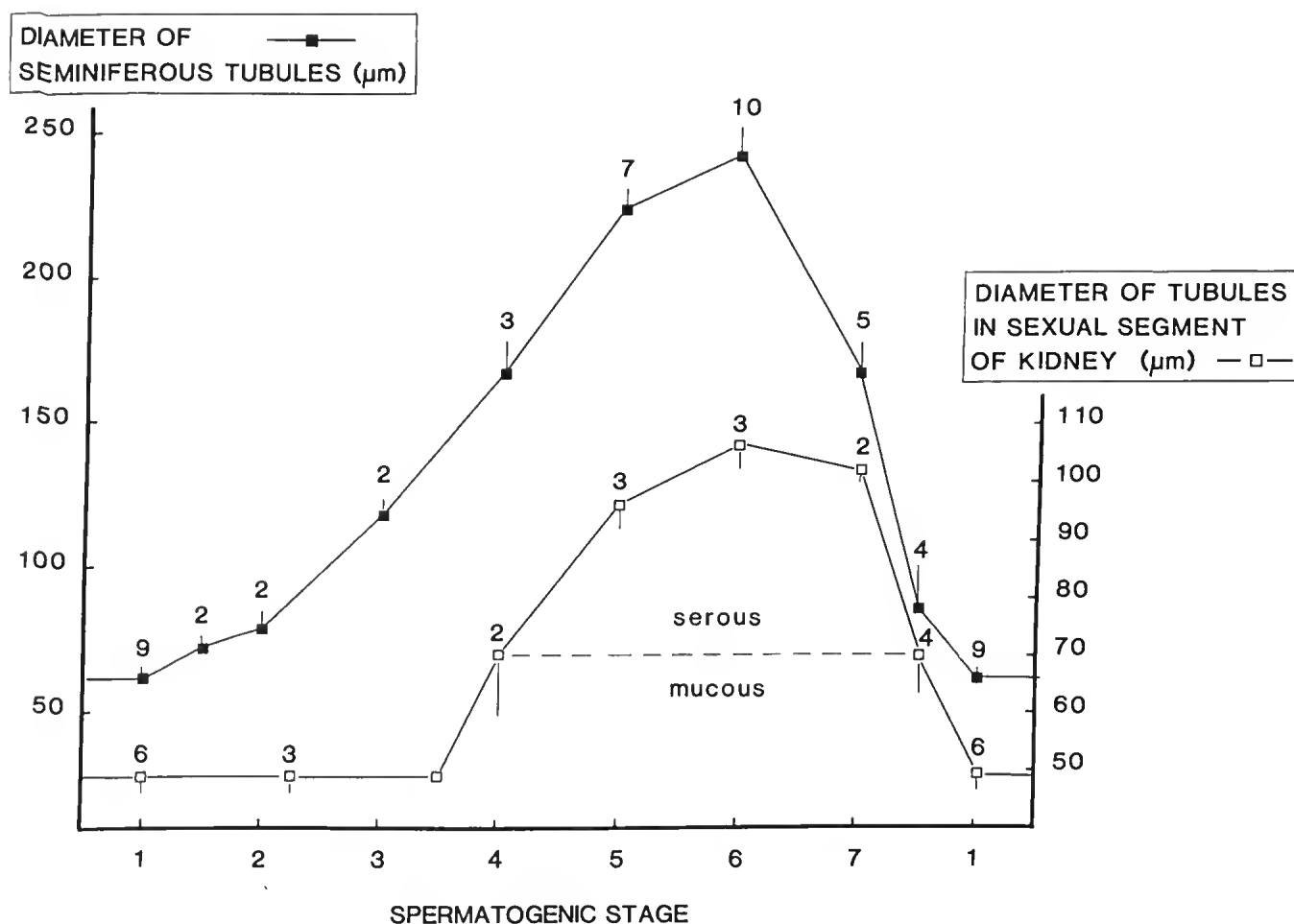
Figure 1 Composite diagram showing the relationship between stage of spermatogenesis and the diameter of the seminiferous tubules as well as that of the collecting ducts in the sexual segment of the kidney. Means (±SD) are given for seven species of aganid lizards from Western Australia showing prenuptial spermatogenesis.

Table 2

Plasma levels of sex steriods in male and female *Amphibolurus mitchelli*, *A. minor* and *Lophognathus longirostris* collected on Mallina Station, near Port Hedland, between 1984-1987. The statistical significance of differences between means within columns is indicated by the P value inserted between the two means concerned.

Species	Date	Sex	No.	Plasma Steriod Levels (ng/ml)			
				Progesterone	DHT	Testosterone	Oestradiol-17β
Amphibolurus *mitchelli*	March 1984	M	4	0.47±0.27 P=0.001	0.68±0.11	7.36±0.73 P=0.009	0.27±0.04
		F	1	5.00	0.25	1.62	0.49
	May 1985	M	1	0.21	1.36	3.27	0.18
		F	1	0.15	0.39	0.20	0.26
	Nov 1985	M	1	0.39	0.39	11.73	0.08
	March 1986	M	8	0.49±0.10 P=0.009	1.37±0.21 P=0.004	4.99±1.11 P=0.009	0.48±0.14
		F	5	1.79±0.52	0.39±0.06	0.53±0.28	0.44±0.14
	Nov 1986	M	1	0.31	4.49 P=0.03	18.14 P<0.001	0.11
		F	2	0.39±0.05	0.98±0.67	1.39±0.57	0.09±0.01
	Dec 1987	M	1	0.92	4.93	17.73	0.02
Amphibolurus *minor*	March 1984	M	1	0.26	0.73	2.77	0.14
	Nov 1984	M	4	0.65±0.20	0.72±0.19	4.13±1.46	0.25±0.02
		F	1	0.50	0.43	0.63	0.17
	May 1985	M	1	0.12	0.34	0.32 P=0.05	
	Nov 1985	M	3	0.51±0.05	0.49±0.03	2.25±0.42	0.17±0.02
Lophognathus *longirostris*	May 1985	M	1	0.54	0.61	0.29	0.37
	March 1986	M	1	1.19	0.72	2.36	0.17

Table 3

Plasma testosterone levels in male *Amphibolurus* species by stage of spermatogenesis (Mean ±SE (n)). P values refer to adjacent means within columns.

Reproductive State	Stage of Spermato-genesis[1]	State of Sexual Segment of Kidney	Plasma Testosterone (ng/ml)			
			A. minor	*A. mitchelli*	*A nuchalis*	*A. caudicinctus*
End of breeding to beginning of sexual quiescence	7-1	S-M[2]			10.65±2.47(5)	10.79±1.19(8) (P=0.001)
Sexual quiescence to commencement of spermatogenesis	1-2	M			NS	37.33±7.71(5)
Deferred reproduction	A[3]	M			18.65±4.01(11) (P=0.005)	NS
Approaching reproduction	3-5	M-S			59.99±20.04(3)	
Early breeding	5	S		15.87±2.07(3) P<<0.001)	NS	
Late breeding	6	S	3.32±0.90(7)	5.44±0.79(13)	35.46±11.42(7)	41.11±7.46(4)

[1]according to Marion (1982)
[2]S = serous and hypertrophied; M = mucous and regressed
[3]see text

would seem to be a pattern characteristic of species of tropical origins, such as *A. caudicinctus* and probably also *Diporophora bilineata*. Of those species which are widely distributed throughout the Australian continent, the gecko, *Heteronotia binoei*, shows evidence of sexual activity by early October, but the pygopodid, *Lialis burtonis*, not before mid-November. Thus, in the one geographic region, species may be found displaying patterns of reproduction which may be classified as either early or late vernal, aestival, autumnal or lasting throughout the entirety of the good season. A similar diversity of reproductive cycles in a single area has been reported by Craig & Shine (1985).

It is possible, in a few cases, to compare the reproductive cycle of a given species in different climatic regions, either from our own material or from information in the literature. So far as lizards from temperate regions are concerned, the reproductive cycle of *T. rugosa* in Perth is virtually identical with that described by Bourne *et al.* (1986) for this species in the north of Victoria in south-east Australia. *A. ornatus*, on the other hand, breeds much earlier in the northerly parts of its range, between latitudes 27°-28°S (Bradshaw 1981), roughly at the sime time as *A. nuchalis* at Shark Bay. This probably reflects the fact that higher environmental temperatures accelerate spermatogenesis at these latitudes and enable these lizards to take advantage of increased food supplies which are typical of the spring period in arid mediterranean regions.

Amongst the desert species, *A. isolepis* lays eggs from September until January-February in the Great Victoria Desert (Pianka 1971), whereas egg-laying appears to be restricted to the period from January to March-April in the Pilbara. In this case it would appear that the reproductive period of the species at any one site is primarily attuned to the rainy season. This is clearly suggested in the case of *A. nuchalis* which evidences precocial vernal breeding at Shark Bay and at Alice Springs, in the centre of Australia, but this may be retarded and become aestival or even autumnal at Mallina Station in the Pilbara, depending upon the quantity and the timing of the rains in any one year.

Unfortunately, we have no comparable data from strictly tropical species with which to compare. In non-arid tropical regions the period of reproduction is often quite prolonged and species may breed in either the wet or the dry season of the year (Barbault 1975, Craig & Shine 1985) but this is manifestly not the case with *A. caudicinctus* which has a very brief but intensive period of reproduction which appears to be cued by cyclonic rain.

The small poly-oestrous oviparous species studied here are typically iteroparous with a short life span coupled with a prolonged period of at least potential reproduction. They appear more able to modulate their reproductive cycles to suit local conditions and, particularly in the arid regions, the timing of adequate precipitation seems crucial. The mono-oestrous viviparous species, which are often much larger and longer lived, probably display less plasticity in their reproductive cycles and it would also be of great interest to study in more detail some of the very wide-ranging species, such as *Lialis burtonis*, which occur throughout the Australian continent and are thus exposed to a great range of climatic conditions.

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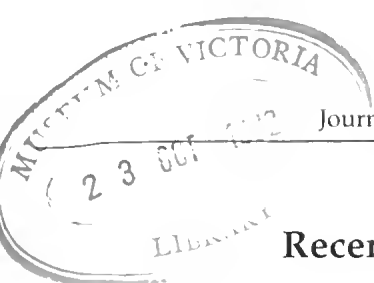
Recent Advances in Science in Western Australia

Life Sciences

The importance of trees as nesting and foraging sites for small, native mammals has been documented by C R Dickman of the University of Sydney. Observations in forests of eastern and western Australia indicate that at least half of all observed foraging occurs on tree surfaces or hollows, loose bark, logs or leaf litter. The requirements of several species are best met by large, mature trees and a complex ground layer that includes logs and leaf litter:

Dickman C R 1991 Use of trees by ground-dwelling mammals: implications for management. In, Conservation of Australia's Forest Fauna (Ed D Lunney) Royal Zoological Society of NSW, Mosman, 125-135.

Analysis by C R Dickman and colleagues of The University of Western Australia and the University of Sydney of the diets of sympatric barn owls *Tyto alba* and Australian kestrels *Falco cenchroides* show that house mice comprised the bulk of the diet of the barn owl, whereas reptiles and insects were the major prey categories in the diet of the kestrel. These dietary differences reflect the diurnal hunting activity of the Australian kestrel and nocturnal hunting, especially for house mice, by the barn owl:

Dickman C R, Daly S J, & Connell G W 1991 Dietary relationships of the barn owl and Australian kestrel on islands off the coast of Western Australia. Emu 91:69-72.

C R Dickman and colleagues, of The University of Western Australia and Sydney University, show that barn owls *Tyto alba* preferentially take small female house mice *Mus domesticus*. Adult mice appear to confine juvenile mice to more open vegetation, where resources are less and the risk of predation is higher:

Dickman C R, Predavec M, & Lynam A J 1991 Differential predation of size and sex classes of mice by the barn owl, *Tyto alba*. Oikos 62:67-76.

The resting metabolism of the desert burrowing frog *Neobatrachus pelobatoides* is shown by J E Flanigan and colleagues at The University of Western Australia to be reduced by 60-70% during aestivation. The metabolism of isolated skeletal muscle was reduced by 70% *in vitro*, indicating endogenous metabolic depression, but other tissues (intestine, liver, skin, fat) did not have an endogenous metabolic depression:

Flanigan J E, Withers P C, & Guppy M 1991 *In vitro* metabolic depression of tissues from the aestivating frog *Neobatrachus pelobatoides*. Journal of experimental Biology 161:273-283.

Whether south-west Australian Restionaceae plants survived fire (resprouter strategy) or were killed (obligate seeder strategy) was determined for 82 species by J S Pate and colleagues of The University of Western Australia, in a wide range of wetland, seasonally inundated and dryland habitats. Resprouters were shown to have larger rhizome diameters, lower culm:rhizome dry weight ratios, and more deeply buried perennating buds. Of the seven recognised categories of rhizome morphology, three were typical of seeders whereas the four were associated more with resprouters:

Pate J S, Meney K A, & Dixon K W 1991 Contrasting growth and morphological characteristics of fire-sensitive (obligate seeder) and fire-resistant (resprouter) species of Restionaceae (s. hemisphere restiads) from South-western Western Australia. Australian Journal of Botany 39:505-525.

The Tammar wallaby was formerly widespread throughout south-western Australia but is now much more restricted in distribution. W E Poole and colleagues from the CSIRO (Lyneham and Canberra) suggest from analyses of cranial morphometrics that there are three major regional groups (Western Australia; South Australian islands; New Zealand) which are apparently all related through a population from Eyre Peninsula that presumably represents the formerly widespread mainland population:

Poole W E, Wood J T, & Simms N G 1991 Distribution of the Tammar, *Macropus eugenii*, and the relationships of populations as determined by cranial morphometrics. Wildl. Res. 18:625-639.

Research by G F Craig, D T Bell and C A Atkins of The University of Western Australia on *Acacia* selected from areas of moderate to high soil salinity indicates that provenances from the most saline sites have greater potential to survive high levels of external salinity in the longer term than those from less saline sites. *A.* aff. *lineolata* and *A. mutabilis* subsp. *stipulifera* proved to be the most tolerant of the ten taxa tested in greenhouse stress tests:

Craig G F, Bell D T, & Atkins C A 1991 Response to salt and waterlogging stress of ten taxa of *Acacia* selected from naturally saline areas of Western Australia. Australian Journal of Botany 38:619-630.

G F Craig and colleagues of The University of Western Australia show, for two strains of *Rhizobium* from nodules of *Acacia redolens* growing in naturally saline areas of south-west Western Australia and two unselected strains from The University of Western Australia's collection, that tolerance of the legume host (*Acacia cyclops* and *A. redolens*) was the most important factor determining the success of compatible *Rhizobium* strains in forming effective symbioses under conditions of high soil salinity:

Craig G F, Atkins C A, & Bell D T 1991 Effect of salinity on growth of four strains of *Rhizobium* and their infectivity and effectiveness on two species of *Acacia*. Plant and Soil 133:253-262.

Analysis of the forage potential of 11 species of *Acacia* from naturally saline areas of Western Australia by G F Craig and colleagues of The University of Western Australia indicates that *Acacia ampliceps*, *A. brumalis*, *A. cyclops* and *A. ligustrina* are the most promising species for use as a perennial fodder shrubs. The ability of salt-tolerant acacias to grow in marginal land means they may provide supplementary forage in times of drought:

Craig G F, Bell D T, & Atkins C A 1991 Nutritional characteristics of selected species of *Acacia* growing in naturally saline areas of Western Australia. Australian Journal of Experimental Agriculture 31:341-345.

Of forty *Eucalyptus* and twenty *Melaleuca* species tested by P G van der Moezel and colleagues of The University of Western Australia, the tolerance of seedlings to salinity and waterlogging was highest for *E. occidentalis*, *E. sargentii*, *E. spathulata*, *E. intertexta*, *E. microtheca*, *E. raveretiana*, *E. striaticalyx* and *E. tereticornis*, and *M. lateriflora*, *M.* sp. aff. *lanceolata* and *M. thyoides*. Matching of suitable species with sites should allow reclamation of saline seeps and provide renewable resources of timber and fuelwood from habitats currently unavailable to agriculture or silviculture:

van der Moezel P G, Pearce-Pinto G V N, & Bell D T 1991 Screening for salt and waterlogging tolerance in *Eucalyptus* and *Melaleuca* species. Forest Ecology & Management 40:27-37.

Little work has been carried out on the systematics of Agaricales in Western Australia, but O K Miller describes eleven new species of *Amanita* mushroom from the southern *Eucalyptus*-dominated forests of Western Australia. All of the species were fruiting in native *Eucalyptus* forests ranging from 247 km north of Perth to Albany, 424 km south of Perth on the southern coast:

Miller O K 1991 New species of *Amanita* from Western Australia. Canadian Journal of Botany 69:2692-2703.

Why has the echidna has been less affected by extensive land clearing and exotic predators than many other mammals of the Western Australian wheatbelt? M Abensperg-Traun of The University of Western Australia attributes the success of the echidna to its widespread habitat use, its specializing on termites and ants that are an abundant and reliable food source for which there is no apparent competition, its metabolic adjustment to drought and fire-induced food shortages, its independence of vegetation for shelter requirements, and minimal predation. Other myrmecophagous mammals in similar environments would experience similar benefits:

> Abensperg-Traun M 1991 Survival strategies of the echidna *Tachyglossus aculeatus* Shaw 1792 (Monotremata: Tachyglossidae). Biological Conservation 58:317-328.

The effect of food distribution on the selection of foraging habitats, and the relationship between food availability, diet, ambient temperature, activity, use of shelter and energy budgets, were studied for the echidna in two Nature Reserves in the wheatbelt of Western Australia by researchers from The University of Western Australia. Food and shelter distribution, and ambient temperature, play important roles in influencing daily and seasonal foraging activity:

> Abensperg-Traun M & De Boer E S 1992 The foraging ecology of a termite- and ant-eating specialist, the echidna *Tachyglossus aculeatus* (Monotremata: Tachyglossidae). Journal of Zoology 226:243-257.

Earth Sciences

A revision of a well-known fossil fauna by R A Henderson of the James Cook University, W J Kennedy of Oxford University, and K J McNamara of the WA Museum examines heteromorph ammonites from the Miria Formation (late Maastrichtian) and a nodule bed (early Maastrichtian) at the top of the underlying Korojon Calcarenite. *Eubaculites* occurs as three biostratigraphically discrete species while *Nostoceras* is restricted to the nodule bed:

> Henderson R A, Kennedy, W J, & McNamara K J 1992 Maastrichtian heteromorph ammonites from the Carnarvon Basin, Western Australia. Alcheringa 16:133-170

In the first comprehensive review of miospores from the well-known Devonian reef complexes of the Lennard Shelf area, one hundred and forty two taxa recorded by K Grey of the Geological Survey of WA, indicate extremely diverse palynofloras, that are correlated with zones erected for the Old Red Sandstone Continent of northeastern Canada and northwestern Europe. The miospores indicated that sedimentation marking the beginning of reef development in some parts of Lennard Shelf had commenced by middle Givetian times:

> Grey K 1992 Miospore assemblages from the Devonian reef complexes, Canning Basin, Western Australia. Geological Survey of Western Australia Bulletin 140.

A regional synthesis of active petroleum exploration by R M Hocking of the Geological Survey of Western Australia, shows two broad trends of lateral fining and upward fining. A number of laterally persistent and essentially synchronous event markers define the stages of deposition within the Jurassic succession:

> Hocking R M 1992 Jurassic deposition in the southern and central North West Shelf, Western Australia. Geological Survey of Western Australia Record 1992/7.

A detailed study of an area of high petroleum prospectivity by K Wulff, of Phillips Australian Oil Company in Perth, subdivides Upper Jurassic syn-rift sediments in the eastern Barrow Sub-basin into five depositional sequences, each separated by regionally correlatable unconformities. Sequence boundary development can be closely related to periods of major changes in basin configuration associated with the sequential breakup of eastern Gondwana. Depositional models integrated with local seismic stratigraphy provide estimates of likely reservoir quality:

> Wulff K 1992 Depositional history and facies analysis of the Upper Jurassic sediments in the eastern Barrow Sub-basin. The APEA Journal 32:104-122.

The Devonian to Lower Carboniferous succession is divided into at least 16 "Vail-type" sequences by a stratigraphic study of rocks associated with the outcropping reef complexes. M J Jackson and colleages of the BMR, Canberra, and Petroleum Securities, Sydney, describe two contrasting phases of development: a reef complex in the Frasnian-early Famennian, and a ramp in the late Famennian-Tournaisian. New and untested petroleum-exploration targets are identified in Famennian-Tournaisian highstand ramps and lowstand fans:

> Jackson M J, Diekman L J, Kennard J M, Southgate P N, O'Brien P E, & Sexton M J 1992 Sequence stratigraphy, basin-floor fans and petroleum plays in the Devonian-Carboniferous of the northern Canning Basin. The APEA Journal 32:214-230.

Note from the Hon Editor: This column helps to link the various disciplines and inform others of the broad spectrum of achievements of WA scientists (or others writing about WA). Contributions to "Recent Advances in Science in Western Australia" are welcome, and may include papers that have caught your attention or that you believe may interest other scientists in Western Australia and abroad. They are usually papers in refereed journals, or books, chapters and reviews. Abstracts from conference proceedings will not be accepted. Please submit short (2-3 sentence) summaries of recent papers, together with a copy of the title, abstract and authors' names and addresses, to the Hon Editor or a member of the Publications Committee: Dr S D Hopper (Life Sciences), Dr A E Cockbain (Earth Sciences), and Assoc Prof J Webb (Physical Sciences). Final choice of articles is at the discretion of the Hon Editor.

"Letters to the Editor" concerning scientific issues of relevance to this journal are also published at the discretion of the Hon Editor. Please submit a word processing disk with letters and suggest potential reviewers or respondents to your letter. *P C Withers, Hon Editor, Journal of the Royal Society of WA.*

Territoriality in a subtropical kyphosid fish associated with macroalgal polygons on reef platforms at Rottnest Island, Western Australia

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Abstract

Kyphosus cornelii, the Western Buffalo Bream, is a relatively large, schooling, herbivorous fish (up to 60 cm total length), endemic to the west coast of Australia, that feeds almost exclusively on rhodophytes. It is shown that individual fish of both sexes defend contiguous, polygonal territories that cover large areas of shallow limestone shoreline platforms. Irregular pentagons and hexagons predominate, delineated by fucoid macroalgal borders that surround areas of predominantly rhodophyte turf. The mean area of each polygon is about 12 m². The majority of polygons have five or six sides and have predominantly six adjacent polygons surrounding them. Territorial macroalgal borders commonly disappear seasonally, but subsequently reappear close to their original positions. Three phases of behaviour are recognised in *K. cornelii*: a territorial phase on shoreline platforms, a schooling phase on the platforms, and a schooling phase in deeper water adjacent to the platforms. The territories appear to be associated with feeding and not directly with breeding.

Introduction

Conspicuous polygons formed by brown macroalgae on intertidal shoreline platforms at Rottnest Island Western Australia (32°00′S, 115°30′E), were first recorded by Playford (1976, 1988), but the reason for their distinctive growth form was unknown (Figs 1-3). Playford (unpublished) had also observed and photographed extensive areas of such polygons on the Houtman Abrolhos, 400 km further north, in 1968. Excavation below the macroalgal borders showed that they were not controlled by joints or other features of the limestone substrate. A clue to their possible link with fish territories was provided by an illustration by Robertson (1989) of "hedgerows" of macroalgae separating territories of the surgeonfish *Acanthurus lineatus* at Moorea in the Pacific. This led to the present study which records that the Rottnest polygons are indeed occupied and apparently maintained as fish territories, by the Western Buffalo Bream, *Kyphosus cornelii* (Whitley 1944).

The aim of this paper is to describe the behaviour of *K. cornelii* in relation to the polygons and to discuss how and why polygons may be associated with its territoriality. Studies of the reproductive biology of *K. cornelii* and detailed studies of feeding in relation to polygon formation and composition of the algal turf within the polygons are proceeding.

K. cornelii is endemic to the west coast of Australia between Cape Leeuwin 33°22′S, 115°08′E and Coral Bay 23°07′S, 113°45′E (Hutchins & Thompson 1983). Shoals of up to several hundred individuals are common on shallow limestone shoreline platforms. It is sympatric over most of its range with *Kyphosus sydneyanus* (Günther 1886), the distribution of which extends to south-eastern Australia (Scott 1962, Hutchins & Swainston 1986) and New Zealand (Doak 1972). Both are relatively large herbivores; *K. cornelii* grows up to 60 cm total length and *K. sydneyanus* up to 80 cm total length (Hutchins & Thompson 1983).

Rimmer (1986) and Rimmer and Wiebe (1987) describe unique digestive tracts and fermentative digestion in these

two kyphosid species. They also show that adults of both species browse exclusively on benthic macroalgae and that the food resource is partitioned, with *K. cornelii* feeding selectively on Rhodophyta (91.9% of diet) and *K. sydneyanus* feeding selectively on Phaephyta (93.9% of diet).

Shoreline platforms fringe most of Rottnest Island and range from a few metres to about 200 m in width. They are cut almost horizontally into eolianite of the Tamala Limestone. According to Playford (1988), their mean elevation is – 0.41 ± 0.11 m Australian Height Datum (AHD, mean sea level) which is about 0.2 m below mean low water level. A platform of this level would be exposed for about 3% of each year (D F Wallace, personal communication).

Hodgkin & DiLollo (1958) described the tides of southwestern Australia in detail and commented on their unusual nature. Tides at Rottnest Island differ little from those at the nearby port of Fremantle (D F Wallace personal communication). They are predominantly diurnal, with only one high and one low water in each 24 hours, with low water at about the same time on successive days, but getting gradually earlier throughout the year. Semidiurnal and mixed tides also occur. However, the daily astronomic tidal range is small, so that atmospheric pressure and wind produce changes of at least the same order of magnitude, making tidal height rather unpredictable. Daily tidal range rarely exceeds 1 m and is generally much lower. Mean annual sea level is about 30 cm higher in winter than in summer. It also varies from year to year over a range of about 15 cm, and Pearce & Phillips (1988) have shown that a high correlation exists between years of low mean sea level at Fremantle and El Nino/Southern Oscillation (ENSO) years, and this is thought to be associated with reduced flow of the Leeuwin Current.

Material and Methods

This work, unless otherwise stated, was undertaken at Wilson Bay on the south side of Rottnest Island. Algal polygons have been photographed (by PEP) at Rottnest Island intermittently since 1976. Photographs from Playford (1988) are reproduced here (Figs 1 and 2) because this

Figure 1. Wilson Bay, October 1985, showing well developed algal polygon formation covering the entire shoreline platform. Reproduced from Playford (1988).
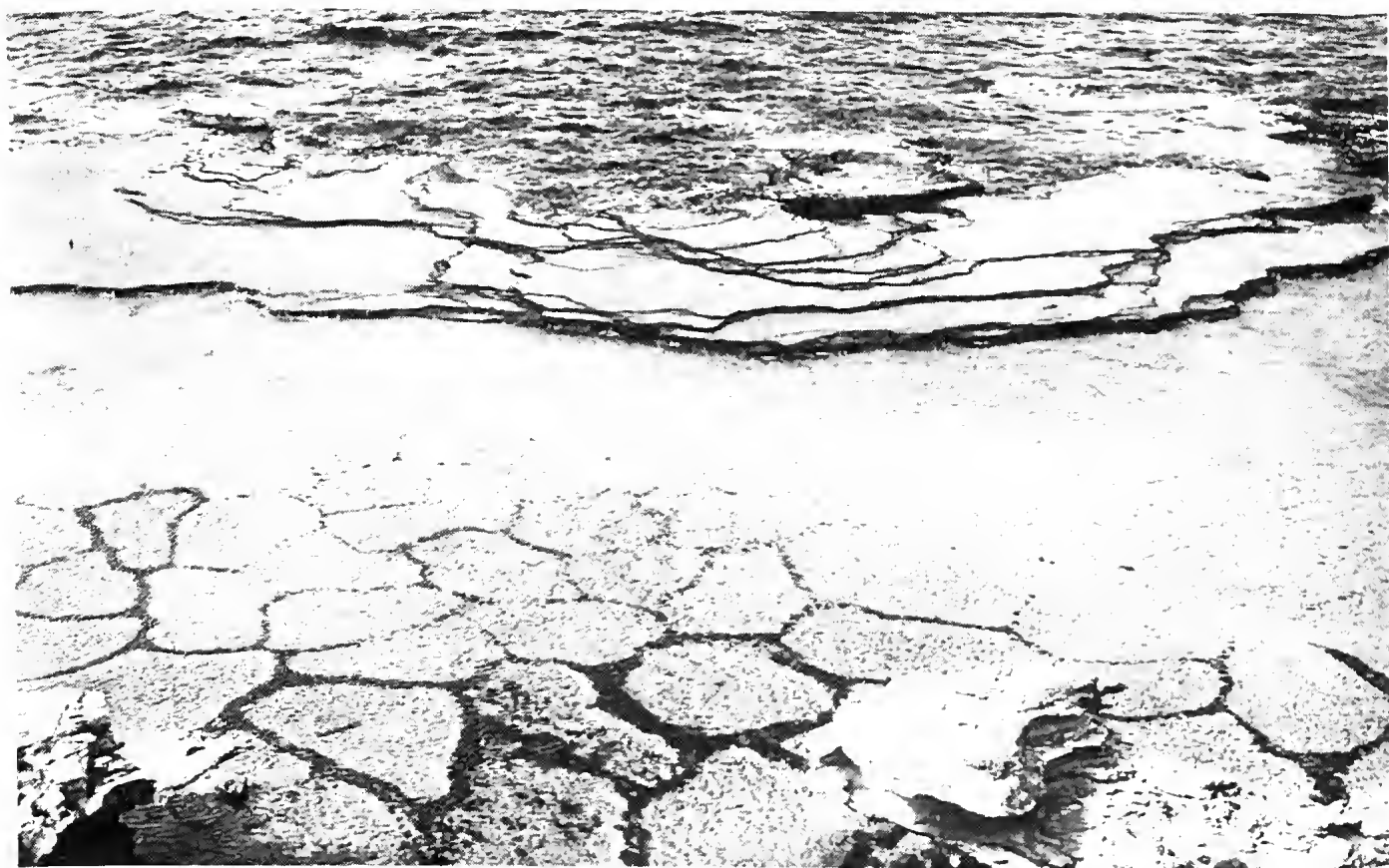
Figure 2. Wilson Bay, January 1988, showing degeneration of algal polygon formation towards the outer shoreline platform. Note the persistence of individual polygons in the same positions from 1985-1988. (The higher level outer platform has raised limestone "paddyfield" terraces which should not be confused with the polygons). Reproduced from Playford (1988).

Figure 3. Aerial view of algal polygons on Radar Reef shoreline platform, Rottnest Island, in November 1991, showing a group of smaller polygons adjacent to the shore.

reference is not readily available outside Western Australia.

The average area of the polygons was estimated from enlargements (x 4) of 1:15,840 aerial photographs (Series WA 1420C, Rottnest Island, 16 October 1972). The number of sides of polygons and the number of adjacent polygons were determined from aerial photographs and photographs taken from cliffs above the shoreline platforms. In determining the number of sides in a particular polygon, the criterion for counting a side, whether straight or curved, was whether it was separated from the next side by a corner, and not by the number of polygons in contact with that side. Thus it was possible for a side to have more than one territory in contact with it. The same criterion was used by Clayton & Vaughan (1982) in their study of mudskipper territories.

Observations and underwater photography of fish were done (by PFB) by snorkelling on 15 separate dates between March 1990 and July 1991 inclusive. The only months not covered during this period were September, December and February. A supplementary sample of eight territorial fish was added in February 1992.

Frequency of browsing and aggressive interactions was scored for individual fish that were each watched for a minimum period of five minutes. These observations were undertaken at the same time of day, thus avoiding possible daily cycles in feeding activity affecting feeding rate scores of territorial and schooling fish.

A total of 33 fish were speared for examination of gonads and stomach contents. Of these 11 were territorial, 2 were schoolers (vagrants) from the reef platform and the balance were from deeper water adjacent to the reef platform. The small number of vagrant fish sampled from the platform

reflects their timid behaviour in shallow water, making them difficult to shoot. Fork length (FL) was measured from the tip of the snout to the middle of the tailfork. Gonads of 24 fish were fixed in 10% formaldehyde for histological examination. Stomach contents of 11 fish were preserved in formaldehyde and examined microscopically and stomach contents of 19 others fish were examined fresh, using a hand lens, to confirm Rimmer & Wiebe's (1987) finding that this species feeds almost exclusively on Rhodophyta.

Results

Description of polygons

Contiguous algal polygons, formed by narrow borders of fucoids (predominantly *Sargassum*) surrounding areas of short (predominantly rhodophyte) turf, covered extensive areas of intertidal and shallow subtidal shoreline platforms in the study area, extending to maximum water depths of about 1.5 m (Figs 1-3). Irregular pentagons and hexagons predominated (Fig 4A). However, the majority of polygons had six adjacent polygons surrounding them (Fig 4B). The mean maximum length was 6.1 m ± 0.89; maximum width (perpendicular to the maximum length) was 3.6 m ± 0.74; and mean area was about 12 m², within a range of about 5 to 20 m². The shared fucoid borders were approximately 10 to 35 cm wide and ranged in height from a few centimetres to approximately 20 cm.

Aerial photographs showed that the polygons within groups tended to be of relatively constant size, but with large size variations from one group to another, sometimes on the same platform (see Fig 3). The approximate average area of individual polygons in the main group at Wilson

Bay (aerial photograph Number 5003, series WA 1420) was 13 m² (ranging from about 10 to 18 m²), whereas in a large group at the eastern end of Strickland Bay (aerial photograph Number 5004) the approximate average was only 7 m² (ranging from about 5 to 9 m²). Elsewhere some groups attained average polygon areas of as much as 16 m².

The degree of development of the fucoid polygon borders varied seasonally, and most polygons gradually degenerated and disappeared (Figs 1 and 2), leaving some areas of the reef platform entirely dominated by turf, only to reappear close to their original positions. This is attributed to regeneration of *Sargassum* thalli from perennial holdfasts.

In 1990-91 both the degree of polygon development and the total area covered by polygons all around Rottnest Island were observed to increase in spring (September-

November) and thereafter to decline. This corresponds with rapid growth of *Sargassum* thalli in spring, culminating in release of gametes in November, followed by senescence and loss of thalli thereafter (G Kendrick, personal communication).

At Wilson Bay the fucoid borders of the polygons in deeper water, towards the outer edges of shoreline platforms, showed more pronounced seasonal decline and were more prone to total disappearance than those towards the shore, which persisted throughout the 1990-91 study period. A comparison of a photograph taken at Wilson Bay in 1976 (Playford 1976) and again in 1988 (Fig 2) demonstrates that the polygons have persisted at Wilson Bay since 1976 in similar positions to those illustrated in 1988. They were still in similar positions during this study.

Polygons were observed to form within extensive (continuous) stands of *Sargassum* between September and November 1990 on shoreline platforms at various localities around Rottnest. By March 1991 most of these polygons had disappeared and some platform surfaces were entirely covered by rhodophyte turf. Aerial photographs taken in March 1990 (Series WA 2851C, 11 March 1990, 1:15,000) similarly showed very few polygons in areas where they were formerly extensive.

Territoriality in Kyphosus cornelii

Three phases of behaviour are recognised in *K. cornelii*: a territorial phase on shoreline platforms, a schooling phase on the platforms, and a schooling phase in deep water adjoining the platforms.

1. Platform territorial phase

Whenever the water level over the shoreline platform at Wilson Bay was greater than approximately 40 cm, each polygon was observed to contain a single, large (> 25 cm fork length) specimen of *K. cornelii* (see Fig 5). Each fish moved about continuously within its polygon, browsing on algal turf, but also interacting aggressively with neighbouring fish along the common macroalgal borders between polygons. The fish faced each other briefly and then swam, sometimes rapidly, for a short distance opposite each other on either side of the border, usually stopping at the nearest corner to face each other again. Territory-holders also showed aggression towards vagrant schools of grazing *K. cornelii* that entered their territories, tending to concentrate on one or two individuals which they sometimes pursued for some distance outside their territories, before returning (see Table 1 for frequency of browsing and aggressive interaction). The shoreline platforms were generally devoid of any other herbivorous fishes, except occasional schools of *Girella zebra* and small (< 15 cm FL) *K. sydneyanus*. The territory-holding fish showed aggression towards *G. zebra* and *K. sydneyanus*, and also *Rhabdosargus sarba*, a bottom-feeding carnivore, but ignored the pelagic, carnivorous Australian Herring, *Arripis georgianus*.

Territory holders were relatively tame, provided that the water depth over the platform was high and the algal borders of polygons were well developed; a fish would generally remain in its polygon despite the presence of a diver, although it became more active. As the water level fell with the tide the fish would become progressively less approachable, and territory holding itself became less pronounced, with fish spending less time in territories and tending to join vagrant schools. Once the water level dropped to approximately 40 cm, very few fish remained territorial. In winter, when polygon borders were poorly developed, territorial fish were extremely nervous and would not remain when a diver entered their polygons, even if water depth was high.
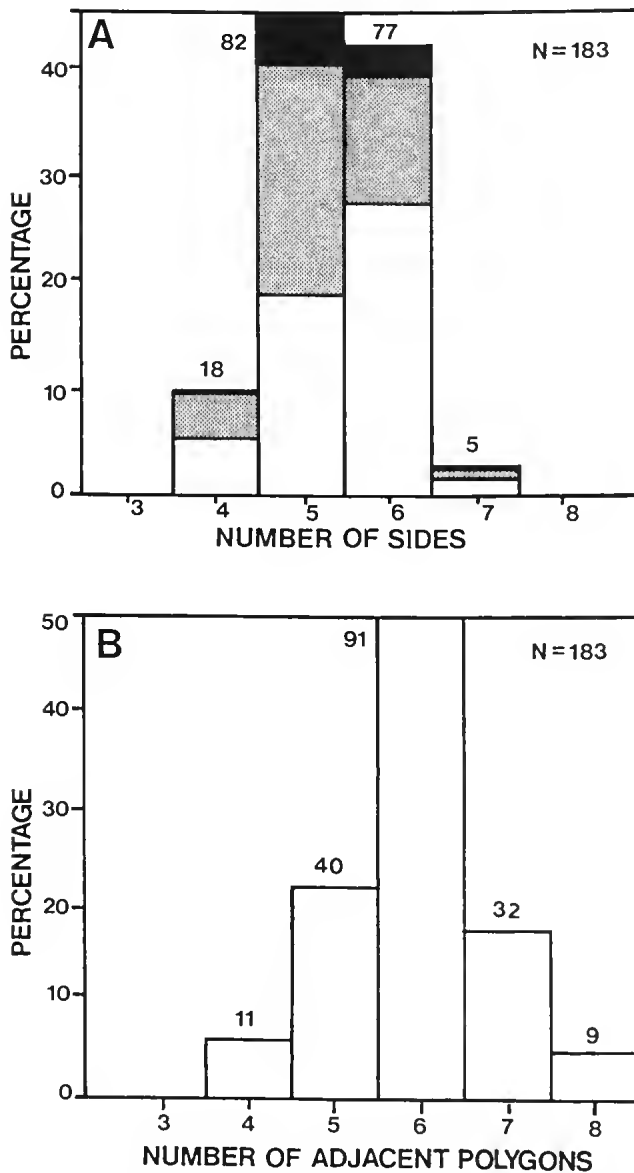
Figure 4. A Frequency distribution of number of sides of algal polygons at Wilson Bay. Shown within each column is the proportion of territories having the same number of adjacent polygons as the number of sides (blank), one more (stippled) and two more (black). B Frequency distribution of number of surrounding, adjacent polygons (neighbours).

Table 1

Comparison of frequency of browsing and aggressive interactions between non-territorial vagrants and territorial fish on shoreline platforms. N is the number of fish observed in each category, SD is standard deviation, t is students t-value, df is degrees of freedom and P is the probability that the means are the same.

	Browsing (Bites/min)		Aggressive Interaction (Encounters/min)	
	non-territorial	territorial	non-territorial	territorial
Mean	1.70	1.68	0.32	1.66
SD	1.64	1.66	0.33	1.03
Range	0-5.2	0-6.4	0-0.6	0-6.4
N	23	19	13	19
t	0.03		− 4.40	
df	40		30	
P	0.979		<0.001	

Territory holders that were shot were replaced by other fish within the hour in most cases, but this requires further study. Preliminary observations also indicate that individuals hold the same territories for prolonged periods, in the order of weeks or even months.

Eleven territory holders were shot, of which six were females (FL 38.8, 36.8, 31.3, 26.4, 41.8 and 31.7 cm) and five were males (FL 36.5, 35.7, 35.8, 34.7 and 40.1 cm). All had full stomachs containing mainly fleshy red algal turf species. The presence of *Sargassum* fragments and plantlets in the stomachs of all territorial fish sampled provides preliminary evidence that brown macroalgae are browsed from within territories, thus maintaining dominance of turf species within the fucoid borders.

The gonads of all territory holders sampled indicated that spawning was imminent or had recently occurred.

2. Platform schooling phase

At the same time that individuals were defending territories, schools of up to several hundred *K. cornelii* moved about continuously, browsing over the entire shoreline platform, including the territorially held polygons. The fish in these schools or aggregations are termed 'vagrants', as individuals within them moved about apparently at random and rather independently of one another. Occasional aggressive interaction between vagrants occurred (see Table 1), but this was not related to a fixed territory. Despite the aggression of polygon territory holders, schools of vagrants were able to feed within territories for brief periods (a few seconds during which some fish were able to take a bite of turf), because the territory-holding fish directed its aggression towards one, usually large, vagrant individual and because vagrants were constantly on the move between territories (see Table 1 for frequency of browsing and aggressive interaction). Schools included both small fish (down to approximately 15 cm FL) and large fish, whereas territorial fish were exclusively large (> 25 cm FL).

Vagrant fish were less approachable than territory-holders, and their timidity increased as water depth over the platform decreased. Once the water depth dropped below approximately 40 cm the schools tended to move over the outer platform edge to adjacent infratidal waters. However, schools continued to feed intermittently on the
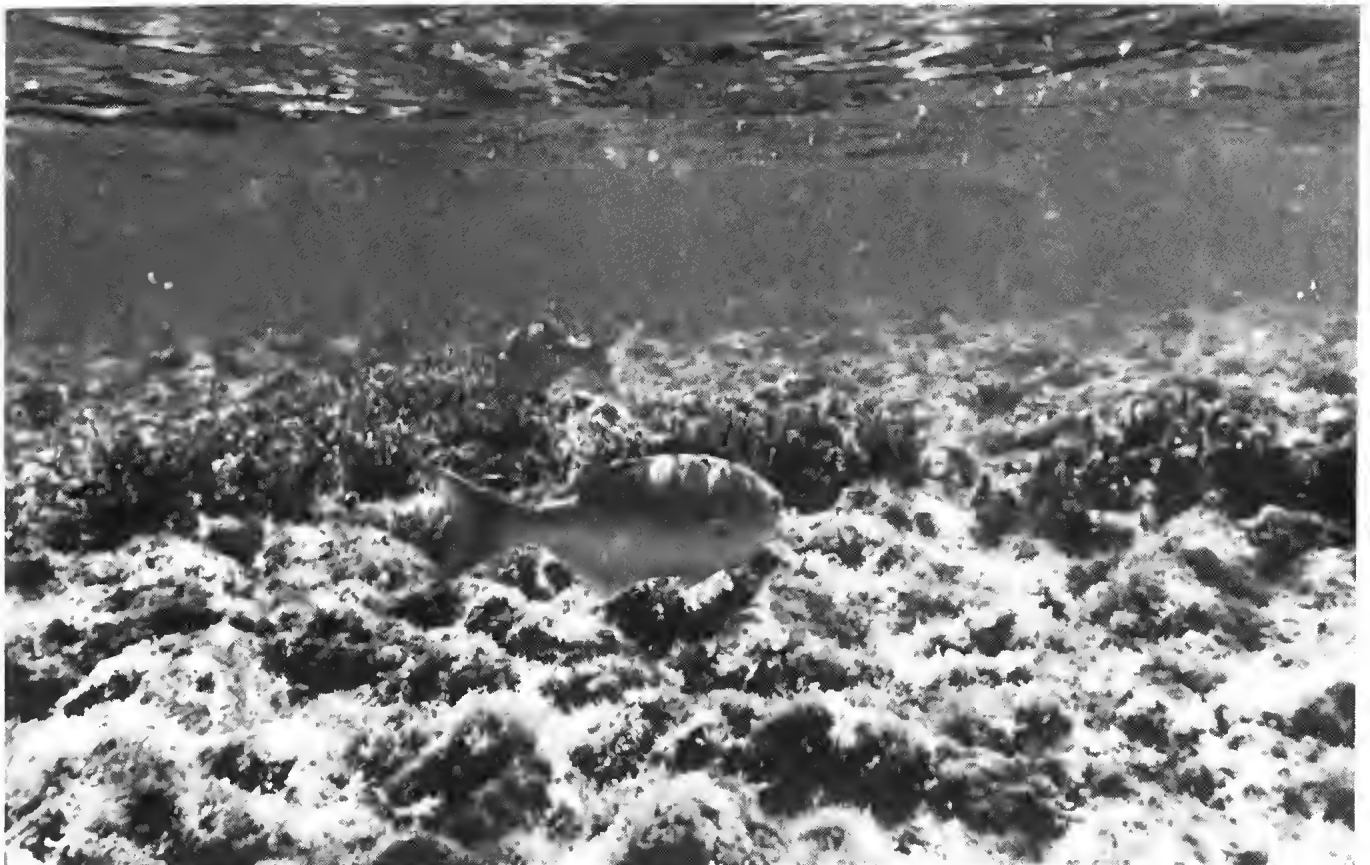
Figure 5. Photograph showing two territorial *Kyphosus cornelii* separated by a fucoid "hedgerow" on the shoreline platform at Wilson Bay, Rottnest Island.

shoreline platform with water depths as low as 30 cm, tending to move on and off with wave surges. Two vagrant fish were shot (FL 47.0 and 32.7 cm). Both were large females and their stomachs were full of predominantly fleshy red algal turf species. The gonads of both were in a ripe, pre-spawning state.

3. Off-platform, deepwater schooling phase

As the water depth over the shoreline platform dropped below approximately 30 cm, all *K. cornelii* moved infratidally and congregated in large schools in the adjacent undercut caves and crevices. These schools, which often intermingled with the infratidal *K. sydneyanus*, appeared to remain within a limited range. Their movements appeared random and aimless; little browsing was observed and individuals occasionally picked pieces of drifting algae from the water column. When disturbed, the fish took shelter in deep crevices. As the water depth over the shoreline platforms increased, fish started to make feeding forays onto the platforms and entered the platform schooling and territorial phases again. Fish in the deep water off the shoreline platforms were relatively tame and easier to sample. Eighteen were shot (FL 27.5-47.4 cm), comprising 8 males and 10 females. All stomachs contained predominantly fleshy red algal turf species.

The cycle of activity described above appeared to be entirely dependent on tidal depth on the reef platforms. Fish were observed to be present on the platform on all three occasions that night dives were undertaken. On one moonlit night they were observed feeding. However, it has not been established whether natural illumination is adequate or necessary for *K. cornelii* to feed on all nights. This cycle of activity contrasts with distinct, regular daily cycles of feeding activity common in herbivorous fishes, for example, marked peaks of feeding in the afternoon (Polunin & Klumpp 1989).

Ripe or spent gonads were recorded in February, March, April, July, October and November, indicating that *K. cornelii* probably breeds throughout the year, although larger samples are required to verify this.

Discussion

Answers as to why and how algal polygons develop on Rottnest Island shoreline platforms are likely to be found in the rather unusual conditions prevailing on them, particularly: the unpredictable and frequently very shallow depth of covering water; the extremely high density and biomass of *K. cornelii* and its relatively large size and high mobility; and the almost exclusive reliance of *K. cornelii* on red-algal turf species for food.

These factors would be expected to result in competition for the food resource and hence the likelihood of behaviour that maximises availability and productivity of palatable red-algal turf species and minimises unpalatable species, including the brown macroalgae that form the polygon borders.

The social behaviour of *K. cornelii* appears to be similar in some respects to that of the parrotfish *Scarus croicensis* from Panama, in which some individuals hold permanent territories while others form feeding schools (Robertson *et al.* 1976). The authors propose that schooling in *S. croicensis* is a mechanism for circumventing territoriality of a competitive, omnivorous damselfish and also territorial conspecifics, as individual schooling fish are attacked less often than non-schooling non-territorials. Given the existence of territoriality in *K. cornelii*, schooling may also allow a higher level of browsing intensity to be achieved.

Reasons for territoriality and algal-polygon formation in relation to *K. cornelii* are not clear. There is no evidence at

this stage, in the form of observations of spawning, that territoriality is directly related to breeding behaviour; also, both sexes were recorded as territory holders. Table 1 shows that there is no significant difference in the rate of browsing between territorial and non-territorial fish. However, each territorial fish benefits from almost exclusive access to a considerable area (5-20 m²/fish, based on the polygon areas), although it engages in significantly more aggressive interactions to achieve this than non-territorial fish. The density of non-territorials (comprising both large and small fish) could not be accurately determined, but it was estimated to be not more than 3 m²/fish, and individuals covered considerable distances in the course of feeding. It is therefore suggested that territoriality may be a mechanism to ensure adequate nutrition for at least a portion of the breeding component of the population.

The reason for the relative constancy in size of algal polygons within individual groups and the variation from one group to another is not known. It could be a function of local rhodophyte productivity, size of fish, water depth, or some other factor. Further work is needed to solve this important question.

In the shallow water covering the shoreline platforms *K. cornelii* is very vulnerable to attack by Ospreys (*Pandion haliaetus*) which have been observed to prey on it. It seems that the macroalgal borders of the polygons may provide some protection from predation on the otherwise bare platforms, as perhaps indicated by the difference observed in tameness of fish in relation to both water depth and
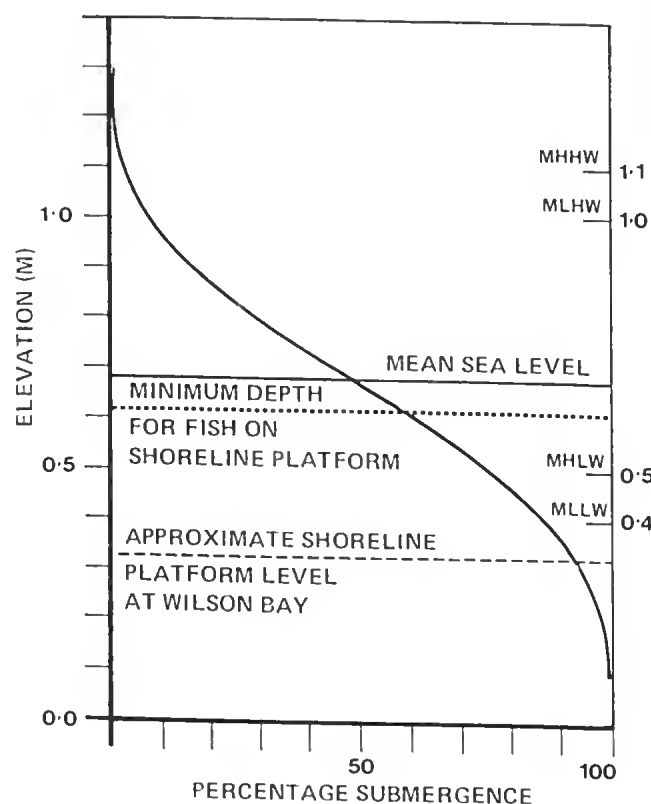
Figure 6. Tidal submergence curve for Rottnest Island showing minimum depth for fish on shoreline platform and approximate shoreline level at Wilson Bay. Elevation refers to height above Tidal Datum (0.0 m). This region experiences a semi-diurnal tidal regime. When two tides occur each day, one is higher than the other. Therefore, the mean higher high water (MHHW), lower high water (MLHW), higher low water (MHLW) and lower low water (MLLW) are indicated separately on the vertical axis.

degree of development of polygon borders. The possible increased danger of Osprey attack when the water depth falls below a critical level (about 40 cm) may also be the reason why the fish desert their territories.

A submergence curve (Fig 6) shows that a relatively small change in mean depth would have a significant effect on the time that K. cornelii is able to spend browsing on the Wilson Bay platform. The 30 cm higher average water level over shoreline platforms in winter would be expected to result in a higher level of browsing and territorial activity than in summer.

Formation and maintenance of the macroalgal borders of the territories must involve behavioural interactions between neighbouring territory holders. Robertson (1989) briefly describes "hedgerows", principally of *Turbinaria*, separating neighbouring territories of *Acanthurus lineatus* in Moorea, French Polynesia, which are the closest approximation to K. cornelii territories we have found in the literature. He suggests that the hedgerows arise because neighbours do not graze along their common territory borders. Because territorial K. cornelii holders browse right up to common territory borders and the demarcation between turf and fucoid borders is so abrupt, it appears that a critical distance may be involved between neighbouring fish below which they do not feed. No displacement feeding activity was observed associated with territorial interactions that could account for the sharp delineation between turf and fucoid borders.

Theoretical reasons for the occurrence of polyhedral and particularly hexagonal shapes in nature have been examined by Thompson (1942). Grant (1968) considered territory shape in terrestrial vertebrates (mainly birds) in structurally simple homogeneous environments and suggested that, theoretically, hexagonal territories will result if territory sizes are similar and neighbours equally spaced. In fishes hexagonal territories have been described for *Tilapia mossambica* (Barlow 1974) and the mudskipper *Boleophthalmus bodarti* (Clayton & Vaughan 1982). At high densities and in a uniform environment the proportion of hexagonal nesting territories in *T. mossambica* increased to 39% at the expense of those with four sides or fewer, but pentagons remained the modal shape with no change in frequency (47%). In *B. bodarti* pentagons also predominated (54%) irrespective of polygon density but there was no increase in frequency of hexagons (30%) at higher densities, which is attributed to differences in territory size. In K. cornelii the frequency of hexagons (42.1%) relative to pentagons (44.8%) is higher than in either of these two species. In addition the modal number of adjacent territories is clearly six (Fig 4B) whereas in *B. bodarti* the mode was five despite some polygons having more adjacent territories than sides. Barlow (1974) indicated that social factors, in addition to the geometrical explanation of efficiency of packing, may play a role in determining polygonal territory shapes. In K. cornelii the distinct mode of six adjacent territories (largely the result of the high frequency of pentagonal territories with one or two more neighbours than sides) appears to support this suggestion. Simultaneous three-fish confrontational interactions were often observed at the "triple junctions" characteristic of the hexagonal and pentagonal polygon arrangement. It is suggested that there may be behavioural reasons favouring

three-way interactions which in turn may determine the angle of corners and number of sides to polygons.

In conclusion, more work is required, not only on the behaviour of K. cornelii, but also on the effect this fish has on the dynamics of benthic reef platform communities at Rottnest Island and elsewhere. Algal polygons have recently been observed at several localities on shoreline platforms between Rottnest Island and the Houtman Abrolhos, and further investigation may show that they are more extensive along this coastline than was previously realised.

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Defoliation of trees in roadside corridors and remnant vegetation in the Western Australian wheatbelt

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Abstract

We compared the abundance and impact of caterpillars of the bag-shelter moth (*Ochrogaster lunifer*) on trees of *Acacia acuminata* on road verges and within a large reserve in the Western Australian wheatbelt. Caterpillars were observed to cause severe damage to roadside trees during an outbreak of the insect in 1987 and 1988. The caterpillars live communally in a bag which develops on a tree branch. Within the reserve, bags were present early in the season but failed to develop and no caterpillars reached maturity. On road verges, the number of bags per tree was significantly greater on narrow verges than on medium or wide verges. An individual colony consumed foliage estimated to be equivalent to that carried by a tree 2 m tall. Colonies were found only on trees greater than 2 m tall, and abundance increased with tree size. Caterpillars significantly affected the numbers of leaves present on tagged shoots on trees in road verges, and defoliated shoots produced a flush of new leaves. Foliar N and P were significantly higher in mature leaves on road verges than in the reserve, and soil N was also higher on road verges. We suggest that ecological processes are significantly modified in road verges, especially narrow verges, compared with intact vegetation, and that this has important implications for corridor management. Intensive management of narrow corridors, or widening of these corridors, is required for their long-term persistence.

Introduction

Despite recent debate about the relative merits of corridors (or linear fragments connecting larger remnants) for nature conservation (Simberloff & Cox 1987, Noss 1987), it is generally considered that vegetation corridors can have many landscape values, both aesthetically and economically, and that they may act as wildlife habitat and as conduits for faunal movement (Harris & Scheck 1991, Loney & Hobbs 1991, Saunders & Hobbs 1991). Because of their importance in the landscape, it is important that we develop an understanding of corridor ecology and dynamics.

Fragmentation of natural landscapes results in the replacement of a continuous cover of native vegetation with a patchwork of vegetation remnants embedded in a matrix which is substantially modified by agriculture or other land uses. The fragmentation process leads to many physical and biological changes, with biota in remnant patches being subjected to altered microclimatic, nutrient and hydrologic regimes, reduction in available habitat and isolation from surrounding areas (Saunders *et al.* 1991). Corridors are particularly likely to be affected by the physical and biological effects of fragmentation due to their high edge:area ratio and their juxtaposition with human transport routes and utilities (Loney & Hobbs 1991). Narrow corridors are particularly open to the influence of the surrounding matrix and can be susceptible to weed invasion, nutrient increase and increased predation risk (Panetta & Hopkins 1991, Cale & Hobbs 1991, Soul & Gilpin 1991).

In this paper, we investigate the possibility that ecological processes are liable to be markedly different between corridor vegetation and vegetation in larger remnant areas. We present a study of herbivory by the bag-shelter moth

(*Ochrogaster lunifer* Herrich-Schaeffer; Lepidoptera, Thaumetopoeidae) on populations of the tree *Acacia acuminata* Benth. on road verges and within a large nature reserve in the Western Australian wheatbelt. This area has been extensively cleared for agriculture over the past century, leaving native vegetation only in relatively small remnant areas and along roadsides (Saunders 1989). Less than 10% of the original native vegetation remains (Beard & Sprenger 1984) and woodland types are poorly represented in conservation reserves. Roadside populations of trees such as *A. acuminata* thus represent an important component of the remaining woodland vegetation. *O. lunifer* is an important defoliator of *A. acuminata* in the Western Australian wheatbelt (Mills 1951, 1952), and of other tree species elsewhere in Australia (Turner 1921, McFarland 1979). It is univoltine, with 6 larval instars occurring from January to June, and adults in November and December. Larvae are gregarious feeders and live together in a bag made of frass and cast skins covered with silk (Van Schagen *et al.* 1992). At the time our study commenced (in 1987), *O. lunifer* was in outbreak, causing severe damage to *A. acuminata* trees on road verges. Caterpillars appear to move freely within individual trees and can also move between trees.

We studied the incidence and impact of *O. lunifer* caterpillars over two years. We assessed the numbers of insect colonies and estimated herbivory levels along road verges and within the nature reserve. We also examined the possible impact of soil and foliar nutrient levels on herbivory. We aimed to assess the differences in herbivore damage between intact vegetation within the reserve and the more disturbed vegetation along roadside corridors.

Methods

This study was conducted in a 20 x 20 km area centred on Durokoppin Nature Reserve (117° 45' E, 31° 24' S), north of Kellerberrin, about 200 km E of Perth, Western Austra-

lia. Kellerberrin has a mediterranean-type climate, with cool wet winters and hot, dry summers and an average annual rainfall of around 340 mm. The wheatbelt region is mainly agricultural land, with numerous small patches of native vegetation interconnected to varying degrees by 'corridors' of native vegetation. Recent estimates indicate that remnant vegetation comprises only 5.7 percent of the 20 x 20 km study area (Saunders *et al.* 1987). Durokoppin Reserve is the largest remnant in the area (1030 ha) and comprises a mixture of woodland, heath and shrubland (Hobbs *et al.* 1989).

A range of sites was selected within the study area. These included stands of *A. acuminata* within Durokoppin Nature Reserve, wide stands of *A. acuminata* along main or minor roads (>20 m wide), verges of medium width along major roads (≈10 m wide) and narrow road verges (<5 m wide) along gravel roads that form a network through the agricultural areas. These minor road verges often contained single rows of *A. acuminata*. Within Durokoppin reserve, *A. acuminata* occurs in open woodland with *Eucalyptus loxophleba* Benth., mostly in isolated patches of 5-10 ha. *A. acuminata* woodland comprises about 4% of the total area of the reserve (Hobbs *et al.* 1989).

In April 1987 and 1988, the conspicuous bag-shelters, which contain the caterpillars of *O. lunifer*, were counted along 100 m transects at 1 km intervals along all of the three types of road verge which occurred in the study area.

Six sites were selected within the study area in early 1987, in order to compare populations of *O. lunifer* in road verges with those in the nature reserve, and also to determine the relationship between tree size and the number of bag-shelters per tree. Three sites were within Durokoppin Nature Reserve and three were on narrow road verges. The trees were divided into five size categories, namely 0-1.9 m, 2-3.9 m, 4-5.9 m, 6-7.9 m and >8 m height, although the latter two categories were absent from the reserve. Six trees of each category were randomly chosen in each of the six areas and the number of bag-shelters per tree was counted.

To determine the amount of foliage consumed by the caterpillars, enclosures made of 1 mm nylon mesh (each 80 x 50 cm) were placed around branches of *A. acuminata* at two sites, one within a dense stand of *A. acuminata* in the reserve, the other along a narrow road verge. Eight trees in each site were selected at random shortly after bag-shelters had been formed (i.e. before significant herbivory occurred) and two mesh enclosures were placed on individual branches, one enclosure containing a bag-shelter with caterpillars and one control without caterpillars (to provide a measure of herbivory by other insects). Each enclosure contained a similar number of leaves. After one week the branches with enclosures were taken back to the laboratory for analysis. Every leaf in each enclosure was examined and the amount of damage was recorded. This procedure was carried out in May and June 1987 and February and March 1988. At the same time, bags were collected from adjacent trees and the number of caterpillars per bag determined. Combining these data provided an estimate of the total amount of damage in a caterpillar season. In order to relate this to the entire tree, leaves were counted on 25 percent of the canopy of 13 individual trees (which did not contain bag-shelters) of various sizes and multiplied by four to obtain total leaves per tree.

Further information on the effect of herbivory on the productivity of *A. acuminata* was obtained by tagging shoots of one year's growth of several trees within the study area. Ten trees were selected within Durokoppin Nature Reserve and ten along a narrow road verge. Five of the trees in each area contained bag-shelter caterpillars, the other five were kept free from caterpillars by removing

bag-shelters and painting Tanglefoot insect repellant gel around the trunks. Five shoots, all at about 3 m height and on the west side of the tree, were tagged on each selected tree. Recordings on each shoot were made at monthly intervals, commencing February 1987, of leaf gain or leaf loss and damage on the shoot.

In order to relate herbivory to the nutrient status of the tree, five samples of soil (top 5 cm), young (new season's) leaves and mature leaves of *A. acuminata* (each sample coming from one tree) were collected from a 50 x 50 m area within Durokoppin Nature Reserve and also from a 100 m stretch of one narrow road verge study site. These samples were dried and analysed for total N, P and K content, using the Kjeldahl digestion method, colorimetry and flame photometry respectively. The data were analysed using t-tests.

Results

In April 1987 there was an estimated total of 10,940 *A. acuminata* trees on verges within the area (Table 1). The number of trees sampled in the 1988 survey was slightly different to the previous year, since 100 m transects were not examined in exactly the same locations. One-way analysis of variance indicated that there was a significant effect of verge width on the number of trees per km in 1987 ($F_{2,212}=4.58$, $p=0.011$) and 1988 ($F_{2,233}=9.96$, $p<0.001$). Comparison of means by the least significant difference (LSD) method indicated that this was due mostly to a greater number of trees in wide verges than in narrow verges in 1987 ($p<0.001$) and 1988 ($p<0.01$). Narrow and medium verges did not differ significantly in tree numbers per km in either year.

The estimated total number of bag-shelters of *O. lunifer* along verges in the area was 15,330 in the 1987 survey but less than 10% of this number in 1988 (Table 1). There was no effect of verge width on number of bag-shelters per km in 1987 ($F_{2,213}=1.32$, NS) or 1988 $F_{2,232}=0.76$, NS). However, verge width did affect the number of bag-shelters per tree in both 1987 ($F_{2,88}=5.03$, $p=0.009$) and 1988 ($F_{2,80}=3.28$, $p=0.043$). This was due to a greater number of bag-shelters

Table 1

Numbers of trees of *Acacia acuminata* and bag-shelters of *Ochrogaster lunifer* along road verges in the study area, estimated from 100 m sections of different types of road verge during April 1987 and 1988 (one sample section per km of road verge type). Tree numbers differ between years because of differences in sections sampled (Mean ± SE).

	Width of Road Verge		
	Wide >20m	Medium ≈10m	Narrow <5m
Length of road system (km)	12.8	34.8	190
No. trees per km 1987	155±33	83±45	32±5
No. trees per km 1988	165±33	96±52	31±5
No. bag-shelters per km 1987	62.5±29.8	31.3±15.2	70.7±12.4
No. bag-shelters per km 1988	4.7±3.1	3.2±1.7	5.2±1.1
No. bag-shelters per tree 1987	0.4±0.3	0.4±0.2	2.2±0.3
No. bag-shelters per tree 1988	0.03±0.02	0.03±0.02	0.16±0.01

per tree on narrow verges than on either medium or wide verges in both years (p<0.05 in all comparisons by LSD). Medium and wide verges did not differ significantly in number of bag-shelters per tree in either year.

There were no bag-shelters in trees <2 m tall on road verges or in the reserve (Table 2). Of the other two possible height comparisons, there were significantly more bags per tree on road verges in the 2-3.9 m height class ($F_{1,99}$=11.35, p<0.01), and no significant difference between road verges and reserve in the 4-5.9 m height class.

Over all 6 plots in the reserve and on verges, mean number of bags per tree was significantly correlated with tree height (r=0.648, p<0.05, n=48) and crown diameter (r=0.632, p<0.05, n=48). Most bag-shelters were located near the top of large, tall trees or near the outside of the canopy, where new foliage is more abundant than elsewhere in the tree.

In the foliage consumption experiment, no differences were found in consumption between branches with and without bags on trees in the reserve at the start of the experiment, and bags failed to develop. Results are thus given only for road verge trees. It was not possible to standardise the number of leaves per enclosure, but the mean number of leaves per enclosure varied only slightly between the four sampling periods (Table 3), and the differences were not significant. From the damage on each leaf, the total amount of damage per enclosure could be calculated in terms of number of leaf-equivalents consumed per enclosure. The mean number of leaf-equivalents consumed per bag-shelter was calculated by subtracting the value obtained for the controls from that obtained for the enclosures with caterpillars. Consumption was highest in February 1988 (mean = 65 leaf-equivalents). From this information, and the mean number of caterpillars per bag, the amount of foliage consumed per caterpillar per day was calculated, and the total amount of leaves consumed per bag per month was estimated. Again most foliage was consumed in February 1988 (mean = 259 leaf-equivalents) and least in June 1987 (mean = 142 leaf-equivalents). The data provide an estimate of the total amount of damage per bag-shelter during a caterpillar season as being equivalent

Table 2

Tree height, crown diameter and number of bag-shelter colonies of *Ochrogaster lunifer* on trees of *Acacia acuminata* of different height classes within the nature reserve and on a roadside (mean ± SE).

Reserve	Height Class (m)				
	0-1.9	2-3.9	4-5.9	6-7.9	>8
Mean tree height (m)	1.48±0.27	3.08±0.49	5.02±0.77	NA[1]	NA
Mean crown diameter (m)	0.57±0.21	1.23±0.14	2.69±0.66	NA	NA
Mean number of bags per tree	0.00	0.20±0.45	3.60±1.93	NA	NA
Roadside	Height Class (m)				
	0-1.9	2-3.9	4-5.9	6-7.9	>8
Mean tree height (m)	1.42±0.39	3.24±0.24	5.24±0.30	6.72±0.43	9.10±0.66
Mean crown diameter (m)	0.64±0.34	1.74±0.62	4.21±0.91	5.93±1.13	5.34±0.47
Mean number of bags per tree	0.00	0.40±0.54	2.60±1.82	3.60±2.07	11.60±3.58

[1]NA = not available

Table 3

Leaf consumption by *Ochrogaster lunifer* in enclosures placed on branches of *Acacia acuminata* on road verges for one week each month during the 1987 and 1988 caterpillar season. All values are mean ± SE (n = 8). Italic figures represent estimates of leaves consumed per bag-shelter per month and of total consumption per colony over one season.

			Numbers of leaves:					
Month	Year	Total leaves in enclosure	Consumed in enclosure with caterpillars	Consumed in enclosure without caterpillars	Estimate of no. consumed by caterpillars in one week	No.of caterpillars per bag (n=5)	Estimated foliage consumed per caterpillar per day (g wet wt)	Estimated no. leaves consumed per bag-shelter per month
January								*129*
February	1988	174±36	73±24	8±4	65	63±5	0.028	259
March	1988	161±27	64±21	8±4	56	59±8	0.026	247
April								222
May	1987	188±42	54±18	9±5	45	22±3	0.055	198
June	1987	146±34	43±16	10±5	33	15±3	0.061	142
Total estimated consumption (leaves per bag-shelter per season)								*1197*

to approximately 1200 leaves. This is equivalent to the total amount of foliage on a tree almost 2 m tall (Fig 1). It is recognized that this estimate is affected by the techniques employed, and that caterpillars in an enclosure may exhibit different feeding behaviour to caterpillars in a normal tree.
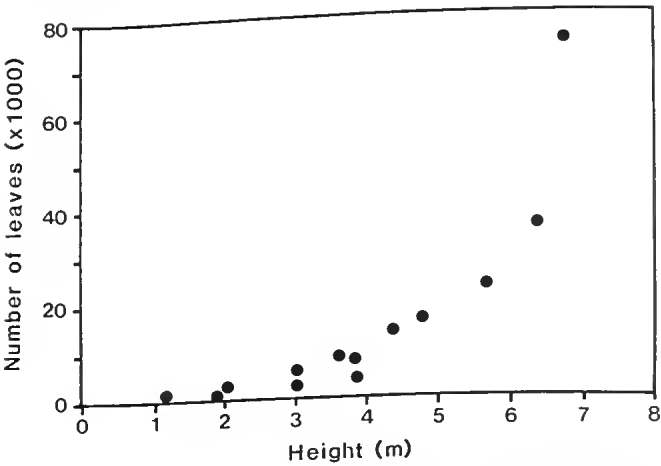
Figure 1. Relationship between height of *Acacia acuminata* trees and number of leaves present. Maximum tree height encountered was <7m.

Shoots on the *A. acuminata* trees on the road verge were longer and supported more leaves than those on trees from the reserve (Table 4). There was generally very little leaf loss on trees from the nature reserve (Fig 2), and there was no significant difference in leaf loss or gain on trees with and without caterpillars. Numbers of leaves per shoot were significantly higher on trees along the verge. The caterpillar-free trees on the road verge followed the same trend as those in the reserve, with very little leaf loss during the experiment. There were, however, highly significant differences in April-July between trees without and trees with caterpillars on the verge (Table 4). An average of 6.9 leaves per shoot were lost and 9.3 leaves per shoot were gained on trees with caterpillars (Fig 2). Here, new growth took place in July, at least two months earlier than on the trees in the reserve and on the caterpillar-free trees of the road verge. Several shoots were completely stripped of leaves, while others lost very few. This depended on their location on the tree; most damage usually occurred on the branch on which the bag-shelter was located.

Levels of N, P and K were higher in young (new season's) leaves than in mature ones in both the road verge and reserve (Table 5). Mature leaves collected from the road verge contained significantly more N and P than those from the nature reserve. No significant difference was detected in levels of K in mature leaves from both areas, and there were no significant differences between
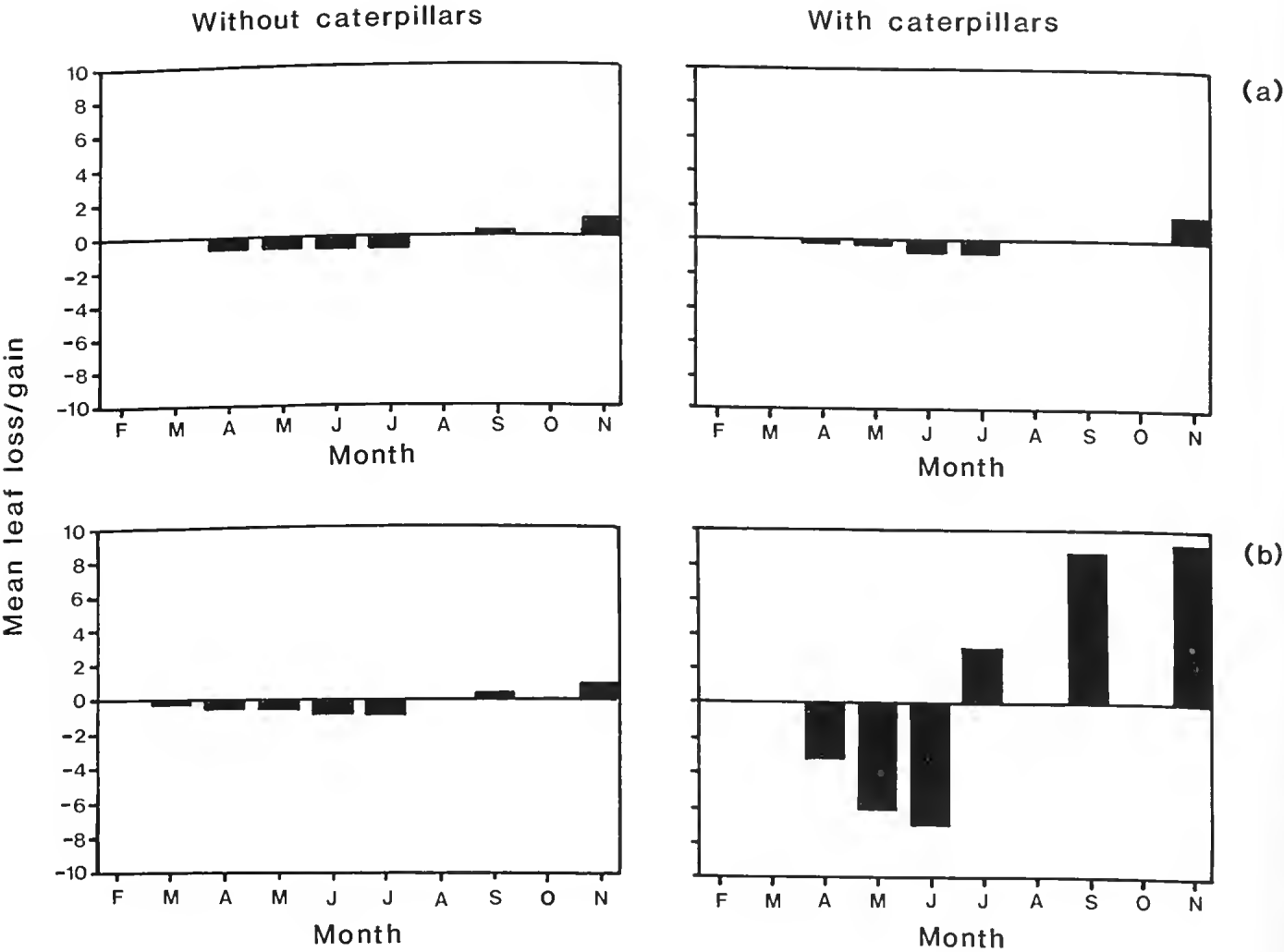
Figure 2. Leaf loss and leaf gain on tagged shoots on *Acacia acuminata* trees with and without the presence of caterpillars in (a) Durokoppin Nature Reserve, and (b) a narrow road verge. No data are available for August and October (n=5).

nutrient levels in young leaves collected from the road verge and those from the nature reserve. Soil samples from road verges contained significantly more N than those taken from within the reserve.

Discussion

The fragmented landscape of the Western Australian wheatbelt has undergone many biotic and environmental changes due to the rapid clearing for agriculture over the last century, and these changes are continuing (Saunders 1989). It is to be expected that large remnant areas will be less affected by these changes than smaller ones (Saunders *et al.* 1991), and it seems likely that smaller areas, and in particular, the long thin strips constituting roadside corridors may be unable to persist in the face of these changes. It is thus important to assess the likely threats to these corridors and determine whether management effort should be put into ameliorating these threats. Our study

illustrates one such threat posed by periodic outbreaks of the moth *O. lunifer* and the resulting defoliation of road verge trees, especially on narrow verges.

The distribution of *O. lunifer* populations in the study area was very patchy in both years studied. No bag-shelters developed fully within the nature reserve, despite the presence of small bags on several trees earlier in the year. In both road verges and in the reserve, there was a preference for taller trees, perhaps because taller trees have more available canopy for moths to lay eggs. Alternatively, the taller trees may offer more foliage as a food source for caterpillars. Our data indicate that trees less than 2 m tall may not provide sufficient foliage for a colony to reach maturity.

In the reserve there was no significant difference in leaf loss and leaf gain between trees with or without caterpillars, since most colonies died out. Pronounced insect defoliation was, however, seen on trees with caterpillars on the road verges. Here, several shoots were defoliated,

Table 4

Mean numbers of leaves (±SE) on tagged shoots of *Acacia acuminata* on reserve and road verge sites in 1987, with and without caterpillars (n=5), and results of t-tests on comparisons between sites (ns=not significant, * p<0.05, *** p<0.001). ND=no data available.

	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Without Caterpillars										
Verge	10.4±0.3	10.2±0.2	9.9±0.3	9.9±0.3	9.6±0.4	9.6±0.4	ND	10.0±0.4	ND	10.6±0.7
Reserve	7.3±0.9	7.2±1.0	6.5±0.6	6.5±0.6	6.4±0.6	6.4±0.6	ND	6.6±0.6	ND	7.4±0.7
With Caterpillars										
Verge	9.8±0.3	9.8±0.3	6.7±0.4	3.8±0.8	2.9±0.8	6.1±1.1	ND	11.7±1.3	ND	12.2±1.1
Reserve	7.1±1.1	7.1±1.1	6.9±1.1	6.8±1.2	6.4±1.2	6.4±1.2	ND	6.5±1.2	ND	8.0±0.8
Verge without vs verge with caterpillars	ns	ns	***	***	***	*	ND	ns	ND	ns
Reserve without vs reserve with caterpillars	ns	ns	ns	ns	ns	ns	ND	ns	ND	ns
Verge without vs reserve without caterpillars	*	*	*	*	*	*	ND	*	ND	*
Verge with vs reserve with caterpillars	*	*	ns	ns	*	ns	ND	***	ND	***

Table 5

Mean nutrient levels ± SE (mg g⁻¹) (n=5) in mature and young leaf and soil samples collected from reserve and verge areas with results of t-tests on comparisons between means (ns=not significant, * p<0.05; ** p<0.01).

Site	Nutrient Level					
	N		P		K	
	Mature	Young	Mature	Young	Mature	Young
Leaves:						
Road verge	35.49±2.47 *	* 43.64±1.49	0.53±0.02 **	** 0.71±0.02	3.46±0.22 **	** 7.82±0.57
Reserve	27.11±0.44 **	ns 41.65±1.56	0.41±0.03 **	ns 0.64±0.03	4.07±0.84 **	ns 8.13±0.31
Soil:						
Road verge	0.40±0.08		0.07±0.01		0.29±0.03	
	*		ns		ns	
Reserve	0.11±0.05		0.07±0.01		0.18±0.03	

resulting in a greater overall leaf loss. However, soon after defoliation new shoots were formed on the trees. On defoliated trees, new shoots were formed in July, whereas on undefoliated trees, this did not happen until September. This resulted in the trees in the nature reserve putting on very little new growth, whereas trees in the verge that were defoliated supported a large amount of new growth, and very little old foliage.

High levels of nutrients, in particular nitrogen, as a result of fertilizer input or other factors have been associated with high insect populations (Port & Thompson 1980, Myers & Port 1981). Investigations have shown that increased nutrient levels, particularly nitrogen, may increase larval development and survival to the adult stage (Mattson 1980, Cates et al. 1987, Landsberg et al. 1990). Young leaves in both reserve and road verge sites contained significantly higher nutrient levels than mature leaves, but mature leaves on road verge trees had significantly greater levels of N and P than trees in the reserve. This was matched by higher levels of soil N on verges than in the reserve, although P values did not differ significantly between verges and the reserve. Elevated N on road verges could be due to sheep urine and faeces, given that sheep are periodically driven along the roads. Cale & Hobbs (1991), on the other hand, found significantly elevated levels of P on road verges compared with reserve areas. There is thus an indication that soil and foliar nutrient levels are higher in the road verges than in the reserve. The relationship between soil and foliar nutrient levels is not clear, however, especially since A. acuminata possesses root nodules containing Rhizobium, a nitrogen-fixing bacterium.

Higher foliar nutrient levels and increased proportions of young leaves may make road verge foliage more attractive to caterpillars, and lead to repeated attacks. Invertebrate herbivory has often been considered a major factor associated with the phenomenon known as 'rural dieback' or 'eucalypt dieback' in Australia (Landsberg et al. 1990). Self-perpetuating defoliation cycles have been hypothesised by Landsberg & Wylie (1983) and Landsberg (1990a) in eastern Australia, while Landsberg (1990b) also hypothesised that increased soil nutrient availability could initiate such cycles. Repeated defoliation could cause severe stress and result in the death of the trees especially if coupled with climate-induced stress (White 1969). Lamont & Southall (1982) have also found that mistletoes are more abundant on A. acuminata trees in road verges than in undisturbed vegetation. This may add a further source of stress to these trees. We noted tree mortality at several of our road verge sites, particularly in narrow verges.

A further factor which may influence insect abundances in road verges versus larger reserves is the relative number of predators. There is little information available on the predators of O. lunifer but there is evidence from other studies that fragmentation and habitat loss have affected the numbers and diversity of insectivorous birds in the area (Lynch & Saunders 1991). Although there is little evidence to suggest that abundance or diversity of insectivorous birds differ greatly between corridors and remnant areas (Cale 1990, Arnold & Weeldenburg 1990), there is a strong correlation between road verge width and abundance of bird species (Arnold & Weeldenburg 1990, Saunders & de Rebeira 1991). This is consistent with significantly greater incidence of bag moths on narrow verges.

Although we were not able to establish the causes of the observed patterns of O. lunifer herbivory, we have shown that trees on road verges, especially narrow verges, are more susceptible to attack than trees within intact vegetation in a large nature reserve. Since caterpillar colonies established but failed to survive within the reserves,

herbivore damage to trees was minimal compared with that found on road verges. The effects of the outbreaks of O. lunifer were thus restricted to road verge tree populations. This observation provides an indication that the dynamics of the road verge vegetation are significantly altered, as has been found in other studies in the area (Cale & Hobbs 1991).

The road verges appear to be much less buffered against disturbing agents, such as the defoliating insects studied here. This is predictable from a consideration of the increased edge effect and influence of the surrounding matrix in corridor vegetation (Saunders et al. 1991, Loney & Hobbs 1991, Soul & Gilpin 1991). Narrow verges, in particular, are at increased risk of losing trees through defoliation. These verges make up by far the greatest proportion of the corridor network in the study area, and this is generally true over much of the Western Australian wheatbelt. This has important implications for the long-term management of these corridors, and brings into question the long-term viability of existing corridor vegetation and of corridors currently being re-established. In order to retain a corridor network in the area, it may be necessary to manage the corridor vegetation more intensively than is necessary in the case of larger remnant areas.

Alternatively, the long-term viability of the narrower corridors may be enhanced by changing their design and structure through the establishment of broader verges, for instance by encouraging farmers to plant several rows of trees adjacent to road verges. This would not only reduce defoliation by O. lunifer but could also benefit the survival and dispersal of native species of conservation interest. In the long term, broader corridors are likely to be more viable in terms of the persistence of their resident populations, and potentially of greater value for species dispersal. Widening of existing narrow corridors is thus an important option to consider in the management of corridor networks. It seems that narrow corridors will not persist in the long term if their populations are reduced by herbivore-induced mortality. If they are considered important within the context of the overall conservation network, they need rapid attention before they disappear.

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Chromosome number, size and interspecific crossing ability of three Old World lupins, *Lupinus princei* Harms, *L. atlanticus* Gladstones and *L. digitatus* Forsk l, and implications for cyto-systematic relationships among the rough-seeded lupins

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Abstract

The chromosome number, size and interspecific crossing ability of several rough-seeded lupins were examined in a breeding programme for domestication of these species. The chromosome number of *Lupinus princei* was found to be n=19 (2n=38), while two other members of the rough-seeded lupin group, *L. atlanticus* and *L. digitatus*, were confirmed to have n=19 (2n=38) and n=18 (2n=36), respectively. *L. princei* had the largest chromosomes of any of the rough-seeded lupins, and failed to produce viable F1 seeds on crossing with *L. cosentinii* (n=16), *L. atlanticus*, *L. digitatus* and *L. pilosus* (n=21). In contrast, *L. digitatus* and *L. atlanticus* produced fertile interspecific hybrids between each other and with *L. cosentinii*. These three species had similar chromosome size. Previous reports indicate that *L. pilosus* and *L. palaestinus* (both n=21, 2n=42) form fertile hybrids and have the smallest chromosomes of the rough-seeded lupins. We confirm that *L. pilosus* does not form fertile F1's with *L. atlanticus*, *L. cosentinii* or *L. digitatus*. All the rough-seeded lupin species studied had high autofertility and pollen viability. Based on this information, we conclude that there are three discernible groups within the rough-seeded lupins: the Princei group (*L. princei*) in equatorial Africa, the Atlanticus group (*L. atlanticus*, *L. digitatus* and *L. cosentinii*) which overlap geographically in north-western Africa, and the Pilosus group (*L. pilosus* and *L. palaestinus*) in the eastern Mediterranean.

Introduction

When Gladstones (1974) reviewed the Old World lupins he resolved them into twelve species, distinguishing the morphologically similar "rough-seeded" lupins (lupins with rough seed testas) from the "smooth-seeded" lupins and describing a new rough-seeded lupin species from Morocco, *Lupinus atlanticus* Gladstones. The rough-seeded lupins have been separated in the genus at the rank of section, Sect. *Scabrispermae* Plitmann & Heyn (Plitmann and Heyn 1984). Systematic relationships within the rough-seeded lupins have been difficult to identify because they are morphologically uniform, and this is exemplified in Gladstones' (1974) description of *L. digitatus* Forsk.: "It has characters in common with *L. princei* and *L. somaliensis* to the south, and with *L. pilosus*, *L. atlanticus* and *L. cosentinii* to the north."

Genomic characters have potential for identifying systematic relationships at the infrageneric level, and the two most widely used characters are chromosome number and crossability. These characters have been used to establish a close taxonomic relationship between *L. pilosus* Murray and *L. palaestinus* Boiss which cross readily and share a chromosome number n=21 (Tuschnjakowa 1935, Kazimierski 1961, Pazy *et al.* 1977, Plitmann *et al.* 1980, Pazy *et al.* 1981). While the chromosome number of *L. cosentinii* Guss. (n=16) has been well established (Malheiros 1942, Gladstones 1958, Pazy *et al.* 1977), *L. princei* Harms has not been investigated and only unpublished reports exist of chromosome numbers for *L. atlanticus* (n=19) (Pazy, unpublished, cited in Plitmann *et al.* 1980) and *L. digitatus* (n=18) (Plitmann and Heyn, unpublished, cited in Plitmann and

Heyn 1984). A report of n=18 also exists for *L. tassilicus* Maire (Eichorn 1949) which is believed to be synonymous with *L. digitatus* (Gladstones 1974). *L. somaliensis* Baker is known only from a single herbarium specimen and although suggested by Gladstones (1974) to be a distinct species, there have been no further records of its existence in Somalia since the original collection was made in the Golis Range before 1895 (M Thulin, Uppsala University, Sweden, personal communication).

An understanding of the interspecific relationships between the extant species in the rough-seeded lupins is essential in a breeding programme to domesticate this group. *L. atlanticus* and *L. pilosus* show potential as crops in Western Australia, especially on fine-textured neutral or alkaline soils (Roy and Gladstones 1983, Gladstones 1984, Buirchell and Cowling 1989). These two species may benefit from domestication genes transferred to them from *L. cosentinii*, which was the first (and as yet, only) rough-seeded lupin species to be fully domesticated (Gladstones 1982).

L. cosentinii was introduced into Western Australia more than one hundred years ago and it quickly became naturalized (Gladstones 1982). Known locally as the "Western Australian Blue Lupin" or "Sandplain Lupin", it occurs in coastal areas of south-west Western Australia. It is often sown into pastures for sheep feed and soil improvement where it regenerates for several years (Gladstones 1958).

In this paper we report the chromosome number of *L. princei*, and confirm unpublished chromosome number records for *L. atlanticus* and *L. digitatus*. The range in size of chromosomes is documented for these species, and the breeding systems of *L. princei*, *L. atlanticus* and *L. digitatus*

are reported. Interspecific crossing data are then used to explore cyto-systematic relationships among the rough-seeded lupin group.

Materials and Methods

The *L. atlanticus* accession used in chromosome determinations, Commonwealth Plant Introduction (CPI) number 65223, originated from the Atlas Mountains of Morocco; the *L. digitatus* accession (CPI 120486) originated from Egypt; and the *L. princei* accession (CPI 120487) originated from Kitali, Kenya. Collection site details are described in Clements and Cowling (1990). Several other accessions were used in interspecific crossing experiments. Seeds are held in the Australian Lupin Collection, and small samples are available upon request from the authors.

Meiosis was examined in pollen mother cells of young anthers from five plants for each species. Bud material was fixed in ethanol:acetic acid (3:1) at 50°C for 1 hr. The buds were transferred to 70% ethanol at 50°C for 1 hr, then bulk stained in alcoholic hydrochloric acid carmine (Snow 1963) for 5-14 days before analysis.

Pollen viability was determined by calculating the frequency of pollen grains that were stained with lactophenol-cotton blue. Autofertility was determined by calculating the percentage of ovules that developed into seeds in a sample of pods from plants that were isolated from insect pollinating vectors in insect-proof glasshouses or screen-houses.

Mitotic metaphases were examined in dividing root tip cells. Seeds were scarified and germinated on blotting paper in petri dishes at 22-27°C for 3-4 days. Root tips were cold treated with or without 0.1% colchicine at 2-3.5°C for 2.5-3.5 hr, then fixed in ethanol:acetic acid (3:1) for 5 min at 50°C, transfered to new fixative and kept at 3.5°C. After 18-48 hr the root tips were hydrolyzed in 0.25 N HCl at 45-56°C for 1.5-2.5 min, then squashed in lacto-aceto orcein (Darlington and La Cour 1962). Metaphase chromosome lengths were determined from photographic enlargements with Vernier callipers.

A number of interspecific crosses were attempted with four different accessions of *L. princei*. Pollen from several accessions of *L. atlanticus* and *L. pilosus* were used along with one accession each of *L. digitatus* and *L. palaestinus* and three accessions of *L. cosentinii*. *L. princei* was emasculated 24 hr prior to pollination when used as the female plant. Reciprocal crosses were also made. Several hundred interspecific crosses were attempted between at least fifteen accessions each of *L. pilosus* and *L. atlanticus*, and a smaller number between *L. pilosus* and *L. cosentinii* or *L. digitatus*.

Results and Observations

Chromosome numbers

We report chromosome counts for three rough-seeded lupin species as follows:

Lupinus princei Harms: n=19 and 2n=38 (Figs 1A and 1B). No previous records exist.

Lupinus atlanticus Gladstones: n=19 and 1n=38 (Figs 1C and 1D). Our determination confirms the only other previous unpublished record of 2n=38 (Pazy, unpublished, cited in Plitmann *et al.* 1980), and establishes that *L. atlanticus* and *L. princei* have the chromosome number n=19 in common.

Lupinus digitatus Forsk l: n=18 and 2n=36 (Figs 1E and 1F). Our determination confirms two previous

counts of 2n=36 (Eichorn 1949 for the synonymous species *L. tassilicus*; and Plitmann & Heyn unpublished, cited in Plitmann & Heyn 1984).

Pollen mother cell meiosis

During metaphase 1 of meiosis, 19 bivalents were regularly observed in all the *L. princei* and *L. atlanticus* plants examined (Figs 1A and 1C respectively). Eighteen bivalents were observed at metaphase 1 in all the *L. digitatus* plants examined (fifty five cells from four plants). No multivalents were observed in any of the cells of the species examined. Anaphase 1 was regular in *L. digitatus* (Fig 1E) and the other two species (forty cells from five plants of each species). Subsequent meiotic stages were also regular in all three species.

Pollen viability and reproductive biology

The observed meiotic regularity was confirmed in pollen viability tests. Pollen stainability for all three species approached 100% (Table 1), which is similar to that determined by Pazy *et al.* (1977) for *L. palaestinus* (96%) and *L. pilosus* (93.6%). We observed that *L. princei*, *L. atlanticus* and *L. digitatus* were all autofertile annual herbs, and set a high frequency of fully developed seed when isolated from insect pollinating vectors (Table 1). It is likely that autofertility, which has also been reported for *L. cosentinii* (Gladstones 1974), *L. pilosus* and *L. palaestinus* (Plitmann *et al.* 1980), accounts for the majority of seeds set in nature by the species we studied.

Root-tip mitosis chromosome sizes and complement symmetry

The lupin species examined in this study had relatively small chromosomes (Table 1) compared with other angiosperms where chromosome lengths may exceed 14 μm (Levin & Funderberg 1979). The chromosomes of *L. princei* are the largest of any lupin species studied to date (compared with Gilot 1965, Pazy *et al.* 1977), and were 1.5-1.65 times the size of *L. atlanticus* and *L. digitatus* chromosomes (Table 1). Pazy *et al.* (1977) determined *L. cosentinii* chromosomes to be about 3 μm in length, which is comparable with the size of *L. atlanticus* and *L. digitatus* chromosomes (Table 1).

The centromeres were in the median and sub-median regions of the mitotic metaphase chromosomes in all the species that were studied. Prominent secondary constrictions (nucleolar organizer regions) and trabants were a feature of a large pair of homologous chromosomes in each species (Figs 1B, 1D, 1F). The chromosome compliments were asymmetrical, and *L. digitatus* had the narrowest range of chromosome lengths (Table 1).

Geographic distribution of chromosome numbers in the rough-seeded lupins

Results from this study and previous reports indicate that chromosome numbers of the rough-seeded lupins are not distributed according to any geographical pattern, and no particular chromosome number is most common for the group (Table 2). *L. atlanticus* and *L. princei* are the two most disjunct species (Fig 2), occurring 5,000 km apart, and share a common chromosome number (n=19). This is in contrast with *L. pilosus* and *L. palaestinus* which also share a common chromosome number (n=21) and whose distributions are contiguous or parapatric. *L. digitatus* is documented to be the most widely distributed rough-seeded lupin species (Gladstones 1974), and it has an intermediate chromosome number for the group.
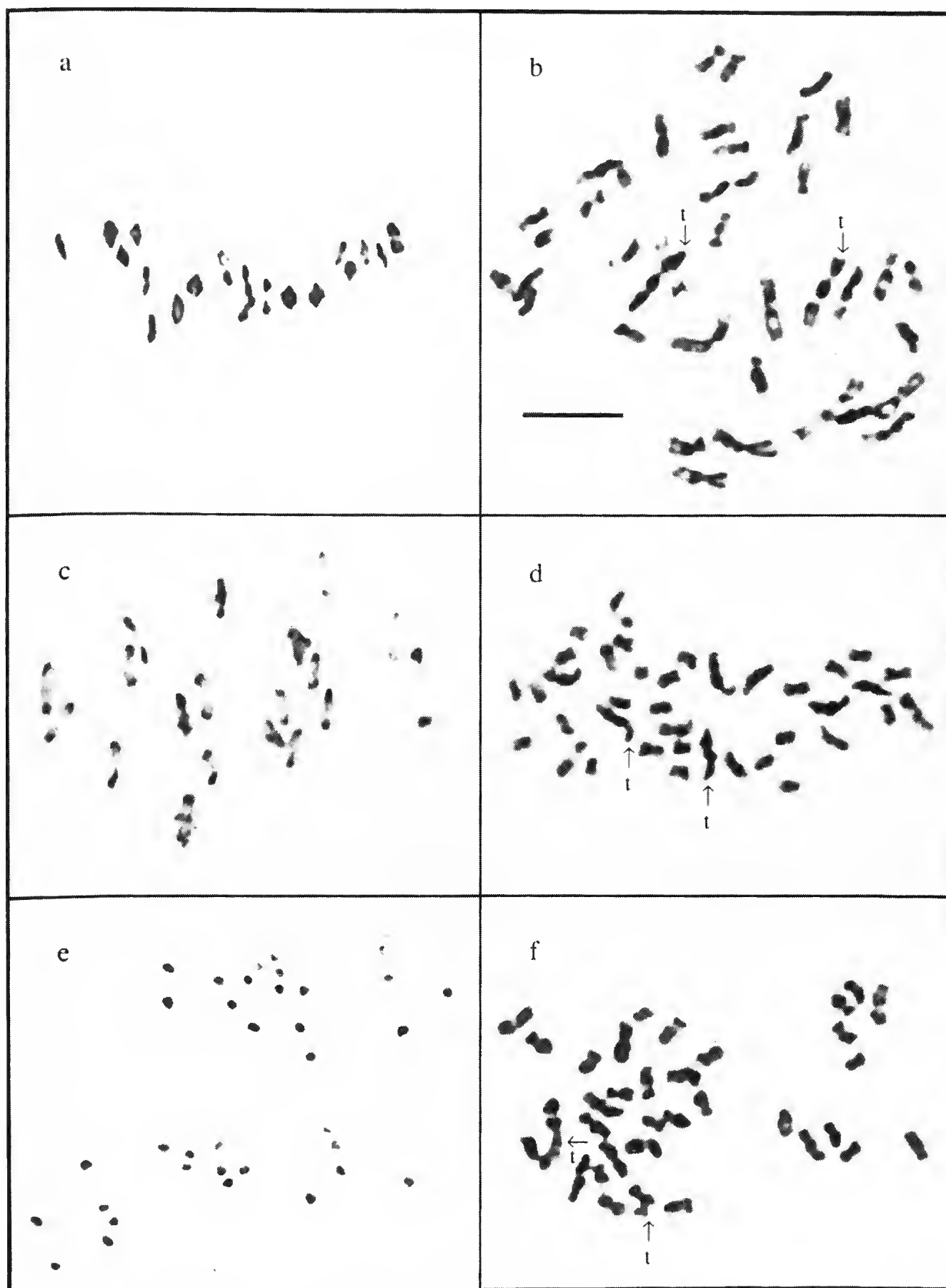
Figure 1. Pollen mother cell meiosis and root-tip mitosis in: **A.** *L. princei*: metaphase I of meiosis, n = 19. **B.** *L. princei*: metaphase of mitosis, 2n = 38. **C.** *L. atlanticus*: metaphase I of meiosis, n = 19. **D.** *L. atlanticus*: metaphase of mitosis, 2n = 38. **E.** *L. digitatus*: anaphase I of meiosis, n = 18. **F.** *L. digitatus*: metaphase of mitosis, 2n = 36. Bar represents 5.5 μm (applies to B, D and F only). Trabants are indicated with the letter 't'.

Crossability of L. princei *with other species*

It was anticipated that *L. cosentinii, L. digitatus* and *L. atlanticus,* which produce viable F1 seeds when crossed to each other (Roy and Gladstones 1985, 1988), would cross to *L. princei* because of the similarity or closeness of their chromosome numbers. However, the results proved otherwise. All interspecific crosses using *L. princei* as the pollen receptor failed to develop fertile F1 seed. Although pod development did proceed, the seeds were shrivelled and lacked an embryo. The reciprocal crosses were also unsuccessful.

Crossability of L. pilosus *with other lupin species*

Interspecific crosses of *L. pilosus* with *L. atlanticus, L. digitatus* and *L. cosentinii* failed to produce fertile F1 plants confirming previous reports of Roy and Gladstones (1988). F1 plants of *L. pilosus / L. atlanticus* or *L. pilosus / L. cosentinii* grew vigorously and flowered profusely but all failed to produce viable seeds. Two F2 seeds, intermediate in size

between the parent seed types, were obtained from one cross of *L. pilosus / L. atlanticus* but these failed to germinate normally and died after radicle emergence and before roots developed.

Discussion

The common chromosome number of *L. princei* and *L. atlanticus* (n=19) has cytogeographic significance for the rough-seeded lupins. Two species sharing the same chromosome number is not unique for the group as *L. pilosus* and *L. palaestinus* both have n=21, but the two cases are different. In contrast to *L. pilosus* and *L. palaestinus,* whose respective geographical distributions overlap, *L. princei* and *L. atlanticus* are geographically separated on opposite sides of the African continent, and occur in different climatic zones. *L. princei* is found in the equatorial highlands of tropical E and NE Africa (Kenya, Tanzania and southern Ethiopia), while *L. atlanticus* grows in the foothills

Table 1

Range of mitotic metaphase chromosome lengths, pollen fertility and autofertility for *L. princei, L. atlanticus* and *L. digitatus*

Species	Range of chromosome lengths (µm)	Pollen viability (%)				Autofertility			
		Mean	Range	No. plants examined	No. ovules	No. pods	No. seed	Fertile ovules (%)	
L. princei	1.77-4.40	98.6	97-99	5	96	26	89	92.7	
L. atlanticus	0.97-3.02	98.0	96-99	3	78	22	76	97.4	
L. digitatus	1.16-2.91	92.4	73-98	11	200	50	175	87.5	

Table 2

Previous chromosome number determinations of the rough-seeded lupins and geographical distributions of the species

Species	Chromosome number	Source	Distribution
L. pilosus Murray	2n = 42	Tuschnjakowa 1935 cf. Gladstones 1958	E. Mediterranean coastal to 1,200 m Greece, Turkey, Syria, Israel
	n = 21	Pazy *et al.* 1977	
L. palaestinus Boiss	2n = 42	Pazy *et al.* 1977	Central and S Israel, Sinai Peninsula—semi-arid to desert regions
	n = 21		
L. atlanticus Gladstones	2n = 38	Pazy (unpublished) cited in Plitmann *et al.* 1980	Morocco, Anti Atlas & foothills of High Atlas mountains—600-1,500 m
	2n = 38	This study	
	n = 19		
L. digitatus Forsk 1	2n = 36	Eichorn 1949 (as *L. tassilicus* Maire)	N. Africa, Egypt, Sahara—few confirmed records (Gladstones 1974)
	2n = 36	Cited in Plitmann & Heyn 1984 (unpublished)	
	2n = 36	This study	
	n = 18		
L. cosentinii Guss	2n = 32	Malheiros 1942	Coastal areas of W. Mediterranean— low altitude; Morocco, Spain and Tunisia
	2n = 32	Gladstones 1958	
	2n = 32	Pazy *et al.* 1977	
L. princei Harms	2n = 38	This study	Equatorial, highlands of Kenya, Tanzania and S. Ethiopia—1,700-3,000 m
	n = 19		
	(No prior determinations recorded)		
L. somaliensis Baker*	(No determinations)		Golis Range in NW Somalia

* *L. somaliensis* was described in 1895 from only one botanical specimen without seeds or pods (Gladstones 1974). The species, if genuine, is now believed to be extinct (M. Thulin, Uppsala University, Sweden, personal communication).

of the Anti Atlas and Atlas Mountains of Morocco where a Mediterranean type climate predominates (Gladstones 1974).

The size of *L. princei* chromosomes, the largest of all the rough-seeded lupins, also sets it apart from *L. atlanticus* and *L. digitatus* (Table 1). Chromosome size variation is potentially a useful taxonomic character (Rees and Jones 1977, Grielhuber 1977, Bennett 1984, Jones 1984) and genomic divergence occurs when the difference in DNA content is large enough to prevent successful crossing between species (Jones 1984).

Finally, *L. princei* failed to produce viable seed when crossed with any of the other rough-seeded lupin species. We conclude, therefore, that the genome of this species has diverged so much from the others that it has been rendered systematically isolated from the rest of the group.

Interspecific crossing between *L. atlanticus* (n=19), *L. digitatus* (n=18), and fully domesticated *L. cosentinii* cv Erregulla (n=16) resulted in fertile F1 progeny in all combinations (Roy and Gladstones 1985, 1988), indicating that they were closely related species. Domestication genes such as soft seeds and early flowering (non-vernalization requirement) were transferred from cv Erregulla to fertile hybrids of *L. atlanticus/L. cosentinii*, and from *L. digitatus* to a fertile hybrid of *L. atlanticus/L. digitatus*, respectively (B J Buirchell unpublished). A comparison of chromosome size, which is about the same for these three species (Table 1), also supports the close relationships among these species.

L. pilosus produces viable F1 progeny when crossed with *L. palaestinus* (both n=21) (Kazimierski 1961, Pazy *et al.* 1977). These two species have the smallest chromosomes of the rough-seeded lupin group, and their geographic range overlaps. Crossability data also indicates that they are distantly related to the other rough-seeded lupins. *L. pilosus* forms sterile F1 plants in crosses with *L. atlanticus* and *L. cosentinii* (Roy and Gladstones 1988, confirmed in this study). *L. princei* failed to produce viable F1 seeds in crosses with *L. pilosus*.

We therefore recognize three subgroups of the rough-seeded lupins based on chromosome number, size and interspecific crossing ability presented here and elsewhere: the Pilosus group with *L. pilosus* and *L. palaestinus*; the Atlanticus group with *L. atlanticus*, *L. digitatus* and *L. cosentinii*; and the Princei group with *L. princei* only. These groupings follow the natural geographic separation of the rough-seeded lupins: the Pilosus group occurs in the east Mediterranean region, the Atlanticus group converges in the vicinity of Morocco, and the Princei group is isolated in eastern equatorial Africa (Fig 2). We tentatively place *L. somaliensis* in the latter group awaiting confirmation of existence of this species in eastern Africa.

We have shown in this study that the rough-seeded lupins are cytologically diverse. They share this feature with the Old World smooth-seeded lupins, whose chromosome numbers are n=20, 25 and 26 from 5 species (Gladstones 1974, Pazy *et al.* 1977). The New World lupins, of which there are over 200 species, contrast in this respect

L. cosentinii	2n = 32	
L. digitatus	2n = 36	
L. atlanticus	2n = 38	
L. princei	2n = 38	
L. pilosus	2n = 42	
L. palaestinus	2n = 42	
L. somaliensis	2n = ?	
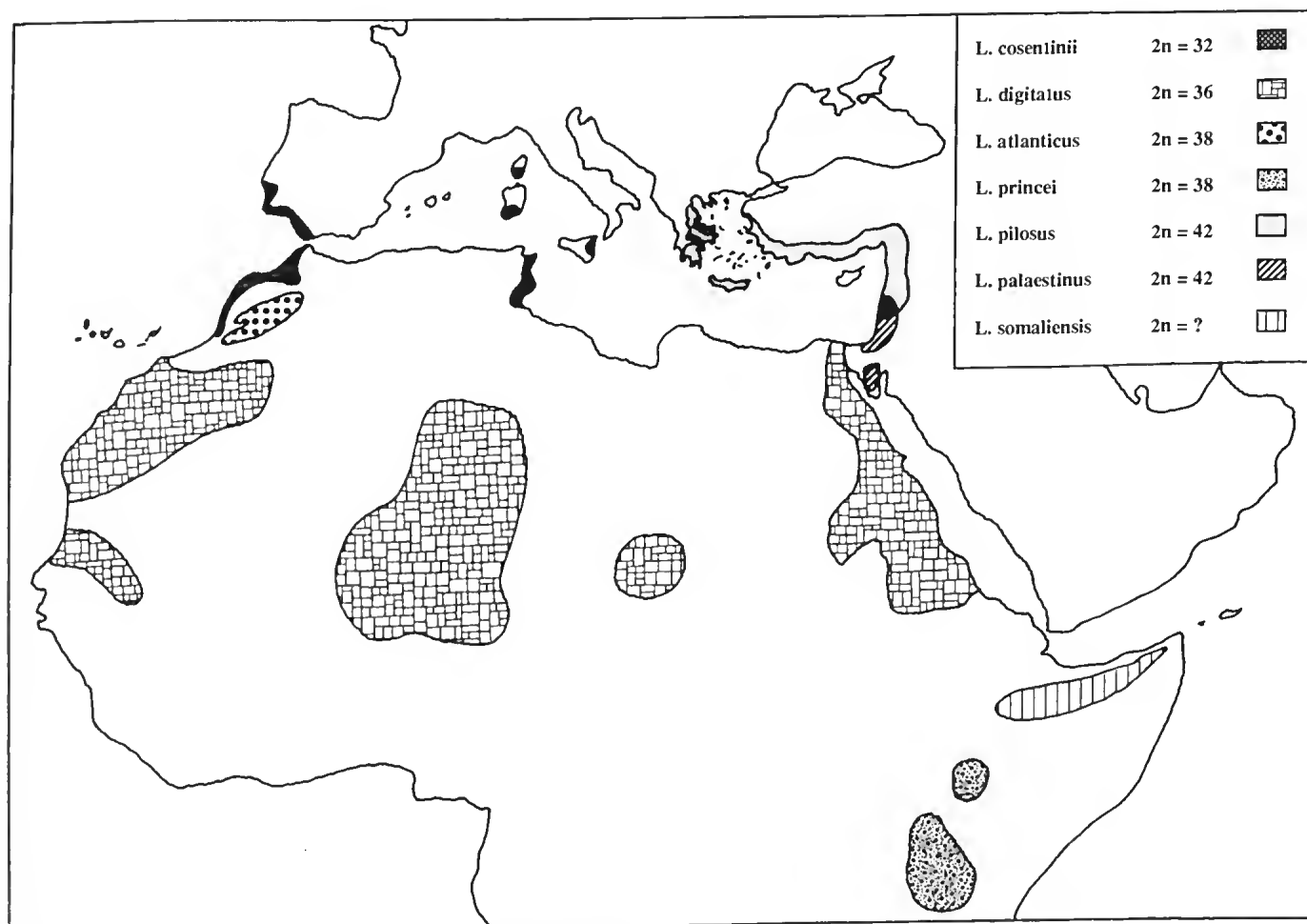
Figure 2. Distribution of the rough-seeded Old World lupins (from Gladstones 1974), with the chromosome numbers of their respective taxa.

with the Old World lupins. The New World lupins are cytologically uniform and characterized by n=24 (Dunn 1984), as well as being typically out-crossing species. This suggests that evolutionary forces operating in the New World have been different from those operating in the Old World. The climate in northern Africa has become drier since the Miocene. As suitable habitat dwindled, the rough-seeded lupins may have became geographically isolated from one another due to their restriction to wetter coastal areas, hills or oases. A consequence of this geographical isolation, reinforced by high autofertility and low gene flow, has been the evolution and conservation of a variety of genomic arrangements in this group, which is in contrast to their morphological uniformity.

Confirmation of the proposed relationships among the rough-seeded lupins will require more detailed karyotype analyses, observation of chromosome pairing in F1 progeny of interspecific crosses, and further interspecific crossing work. Some of this work is currently underway as part of a domestication programme for *L. atlanticus* and other rough-seeded lupins (Buirchell & Cowling 1989).

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Ants as indicators of disturbance at Yanchep National Park, Western Australia

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Abstract

Undisturbed sites at Yanchep National Park support ant communities which, in terms of species richness, evenness and functional group profiles, are typical of undisturbed sites elsewhere in south-western Australia. Slight modifications of the ecosystem result in slight alterations in ant communities. Replacement of native vegetation by gardens or plantations results in a considerable reduction in species and generic richness, reduction in the number of functional groups and altered species composition. Particular species of *Crematogaster*, *Tapinoma* and *Iridomyrmex* are indicative of relatively undisturbed sites, while particular species of *Melophorus* and *Tetramorium* are indicative of highly disturbed environments. Species richness of ants at undisturbed sites is not significantly correlated with numbers of vertebrate species at those sites.

Introduction

Ants are increasingly used as bio-indicators in studies of minesite rehabilitation, fire management, pesticide contamination, habitat disturbance and in theoretical considerations of reserve design (Andersen 1987, 1990, Majer 1983). They are of use in this respect because they are a diverse group of animals with a community structure which tends to reflect the nature of the environment in which they occur. In addition, the diversity and types of ants present are often correlated with the composition of other components of the invertebrate fauna (Majer 1983). Thus although many other invertebrate taxa would also respond to changes in the environment, a consideration of the ant fauna can tell us much about the trends in these other taxa. Ants are also sensitive and react quickly to ecological change (Andersen 1990), interact in many ways with other parts of the ecosystem, occupy a broad range of trophic levels, occupy varied niches and presumably influence a wide range of flora and fauna groups, although the nature of such relationships at a community level has not been elucidated. Ants are also better known taxonomically than many other groups of Australian invertebrates and are readily sampled. Information on distribution, relative abundance and community organization of ants can therefore be interpreted in the context of a whole array of ecological characteristics of the environment (Andersen 1987). Other groups of organisms, such as plants, could be surveyed in order to detect environmental change. Such studies, particularly integrated studies of vegetation structure and floristics, can provide much useful information about the ecological status of an area. However, data on ants can complement such information and, because the presence or absence of ants is influenced by a whole range of factors, can be used to integrate information on a wide range of environmental parameters.

The present study was initiated with the aim of investigating the structure of ant communities in disturbed and undisturbed sites in and near Yanchep National Park (31°32'S, 115°41'E), on the Swan Coastal Plain, near Perth, Western Australia. The only previous systematic sampling of ants in non-urban parts of the Swan Coastal Plain is by

Rossbach & Majer (1983), who suggested that vegetation and soil type each played an important role in determining ant community composition in this area. They also suggested that the trends found in their study may also be discernible in other animal taxa.

Yanchep National Park is 50 km north of Perth. The area, first made a reserve in 1905 for 'Protection and Preservation of Caves and Flora and for a Health and Recreation Pleasure Resort' and vested in the Caves Board, became a National Park in 1969 (National Parks Authority, undated). However, as its main function in its early years was for recreation, some areas of native vegetation were replaced by parks and gardens, and other areas became invaded by weeds. To date, 71 weed species have been recorded in the study area (G J Keighery personal communication).

We set out to determine how the structure and composition of ant communities in disturbed environments in the Yanchep area differed from those in nearby relatively undisturbed native vegetation. It was expected that this would enable us to identify species which could be used as indicators of disturbance. Such indicators would then be of use in future studies when ecological disturbance is being investigated. We also wished to make comparisons between ant distribution patterns and vertebrate distribution patterns for ten sites for which there were pre-existing data on vertebrate animal occurrences (A H Burbidge & J K Rolfe unpublished data).

Methods

Study sites

Most of the study area is on the Spearwood Dunes with a small area on the western boundary being on Quindalup Dunes (Churchward & McArthur 1980). A soil map of the area, drawn from the data of W M McArthur, is shown in Smith *et al.* (1989). Vegetation is primarily woodlands and heaths (D Lamont in Smith *et al.* 1989). Rainfall in the area averages 750 mm per annum with most rain falling between April and October. The average maximum temperature is about 24°C and the average minimum 12°C (Bureau of Meteorology 1966). Ten disturbed sites and 10 undisturbed sites were sampled in and near the National Park

(Fig 1). The vegetation at each site is briefly described in Table 1.

Sampling

Ants were collected by pitfall traps, diurnal hand collections from the ground and vegetation (1.5 person hours per plot), and Winkler-sack extraction from the leaf litter (10 l of litter sampled per plot). At each site, 10 pitfall traps (1.8 cm internal diameter x 17 cm depth) were placed 10 m apart on a single 100 m transect. At sites where vertebrate sampling has been done (see Table 1) (A H Burbidge & J K Rolfe unpublished), the ant sampling transect was placed parallel with, and close to, the vertebrate pit line. Ant pitfall traps each contained about 3 ml of 8:2 (v:v) alcohol-glycerol mixture, which is not attractive to ants (Greenslade & Greenslade 1971). Pitfall traps were left open for seven days in late December 1989, with the other sampling methods being used in late December and early January. The weather was hot and dry during the sampling period.

Representative specimens of ants collected are held at the Wildlife Research Centre, Department of Conservation and Land Management, Woodvale. Collections which could not be assigned a specific name were assigned a species number unique to this study.

Analysis

Species richness for each site was derived by summing the total number of species obtained from pits and hand collections. Species evenness for each site was calculated following the method outlined by Majer (1983) and Rossbach & Majer (1983), using the formula

$$J' = \frac{H'}{\log S}$$

where H' is the Shannon-Weaver diversity index (Shannon & Weaver 1949) and S is the total species present.

Table 1

Vegetation at each sampling site in and near Yanchep National Park. The soil classification is that of McArthur, as shown in Smith *et al.* (1989). Vegetation classification is based on that of D Lamont, shown in Smith *et al.* (1989). Vertebrates have also been sampled at sites marked with an asterisk. Words in bold type are the basis of the site codes.

Site code		Vegetation
This study	CALM[1]	
Q1*	9A	**Quindalup** dune vegetation with scattered *Acacia saligna* and *Xanthorrhoea* over shrubs to 1 m and herbs on Quindalup sands.
Q2*	9C	**Quindalup** dune vegetation with very sparse *A. saligna* over shrubs to 1 m and herbs on Quindalup sands.
D1*	4B	Mid-dense **Dryandra** heath to 2 m of mainly *Dryandra sessilis* over low shrubs of various species with herbs in more open areas, on Karrakatta limestone.
D2*	5B	Mid-dense **Dryandra** heath to 2 m of *D. sessilis* and *Hakea trifurcata* over low shrubs of various species with herbs in more open areas, on Karrakatta limestone.
B1*	2A	Low **Banksia** woodland to 8 m of *Banksia attenuata* and *B. menziesii* with scattered *Eucalyptus marginata* and *E. todtiana* over heath to 2 m with some herbs on Karrakatta sands.
B2*	6B	Open low **Banksia** woodland to 8 m of *B. attenuata* and *B. menziesii* over heath to 2 m with some herbs on Karrakatta sands.
J1*	3A	Low **Jarrah** woodland to 15 m of *Eucalyptus marginata* and *Banksia attenuata* over shrubs to 2 m with some herbs on Karrakatta sands.
J2*	7B	Low **Jarrah** woodland to 15 m of *E. marginata* and *B. attenuata* over shrubs to 2 m with some herbs on Karrakatta sands.
T1*	8B	Woodland of **Tuart**, *Eucalyptus gomphocephala*, over low woodland of *Jacksonia* and *Acacia* shrubs to 4 m and sparse herbs on Spearwood sands.
T2*	10B	Woodland of **Tuart**, *E. gomphocephala*, over low woodland of *Eucalyptus*, *Acacia*, *Melaleuca* and *Banksia* and shrubs to 4 m with patches of herbs on Spearwood sands.
HD	E	Scattered shrubs in **heath, disturbed** by past human activity, to 3 m of *Conospermum* and *Acacia rostellifera* over shrubs to 1 m of mainly *Hakea prostrata*, *Grevillea vestita*, *Dryandra nivea* and *Jacksonia stricta* adjacent to tuart woodland on Karrakatta sand with outcropping limestone.
TD	T	Woodland of **Tuart, disturbed** by previous grazing and simplification of understorey; *Eucalyptus gomphocephala*, over sparse understorey of *B. grandis* to 5 m and *G. vestita*, *Macrozamia riedlei*, *Solanum sodomaeum* and scattered herbs, particularly *Carpobrotus* and *Ehrharta*.
BG1	BG1	Low woodland, disturbed by trampling and weed invasion, adjacent to **Boomerang Gorge**; *Eucalyptus gomphocephala* over shrubs of *Spyridium globulosum* and *Hibiscus huegelii* to 6 m with smaller shrubs, particularly *Acacia pulchella* and herbaceous weeds including *Myrsiphyllum asparagoides* and *Ehrharta breviflora*.
BG2	BG2	Low woodland, disturbed by trampling and weed invasion, in **Boomerang Gorge**; *E. gomphocephala* over shrubs of *S. globulosum* and *H. huegelii* to 6 m with smaller shrubs, the sedges *Lepidosperma gladiatum* and *L. tenne* and weeds including *M. asparagoides* and *Conyza bonariensis*.
G1	GL	**Garden** comprised of woodland of *Eucalyptus* spp. (mostly *E. gomphocephala*) and *Banksia littoralis* over mowed and watered lawn.
G2	R	**Garden** comprised of woodland of *E. gomphocephala* and *Agonis flexuosa* over mowed and watered lawn.
EP1	K	**Eucalypt plantation** (low woodland) of *Eucalyptus rudis*, *E. robusta* and *E. globulus* over low sedges and herbs, especially *Pelargonium capitatum*, on Beonaddy sand.
EP2	MG	**Eucalypt plantation** (low woodland) of *E. viminalis*, *E. robusta*, *E. camaldulensis* and *E. globulus* over low sedges and herbs on Beonaddy sand.
P1	P1	Low **pine** forest (plantation) of *Pinus pinaster* to ca. 10 m over rare *Macrozamia riedlei* on Karrakatta sands.
P2	P2	Ditto, about 200 m away.

[1] CALM = WA Department of Conservation and Land Management; site codes in this column have been used for CALM purposes and for the vertebrate and vascular plant survey, but have been simplified to those in the first column for the present survey.
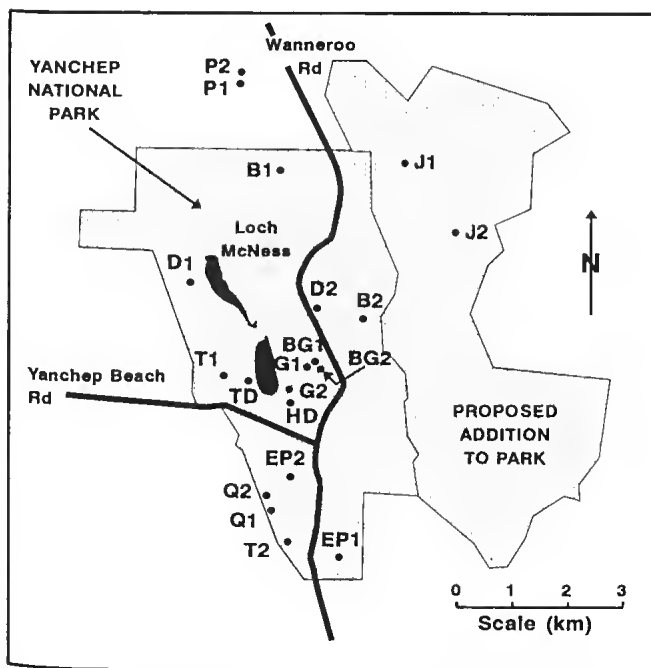
Figure 1. Location of sites used to sample ants in and near Yanchep National Park.

Ants collected from pitfall traps were classified into Greenslade's community structure categories (see Greenslade & Thompson 1981 and Andersen 1987, 1990).

Multivariate analyses were carried out using the computer package PATN (Belbin 1989, 1991a) in order to elucidate the relationships between sites in terms of the ant species which were present. Initially, a cluster analysis technique (classification) was used to detect similarities between sites and to determine the degree of similarity between disturbed and undisturbed sites. Sites were classified in terms of ant species presence using the Bray-Curtis (Czekanowski) association measure for presence-absence data, followed by hierarchical agglomerative fusion classification (flexible UPGMA, $beta = -0.1$). This procedure is appropriate for ecological presence-absence data and is robust to variations in species abundance patterns and hence sampling efficiencies (Faith *et al.* 1987, Belbin 1991a).

The data were then subjected to an ordination procedure to provide an independent measure of similarity between sites. Sites which are close together in the ordination space will be those which are similar in species composition. Ordination was carried out using the procedure SSH (semi-strong hybrid multidimensional scaling) (Belbin 1991b), which is robust to species richness effects. This was followed by principal axis rotation in order to maximize the variance on each axis. In order to facilitate interpretation of the observed patterns, ant species were also classified in terms of the sites at which they occurred. This was done using the two-step association measure of Belbin (1980) as this measure is robust for use in situations such as the present one where sites vary greatly in their levels of species richness (Austin & Belbin 1982). A two-way table was constructed from the classifications of sites and ants, in order to facilitate interpretation of both classifications.

Initial analyses showed that species which occurred at a single site were rare or undersampled species which occurred randomly in the data set. Such species contribute little to estimation of similarity between sites or interpretation of pattern in the data, and therefore were excluded from further analyses.

Data on vertebrate species occurrence are available for the undisturbed sites (A H Burbidge & J K Rolfe unpublished). Numbers of species of vertebrates (reptiles, birds, mammals and all vertebrates combined) were compared with ant species richness using the Spearman rank correlation procedure.

Results

Species abundances, richness and evenness

A total of 111 species from 31 genera were sampled from the sites. The number of ant species within each genus, and also various ant community variables are shown in Table 2.

The total ant species per site (species richness) varied from five to 28. Scanning across Table 2, the first 10 sites may be regarded as relatively undisturbed, the next four as modified native vegetation and the last six as replaced ecosystems. Ant species richness respectively varied from 15-28 and 16-23 in the first two groups of sites. These ranges of values are respectively indicative of undisturbed or slightly disturbed sites which have been sampled at this intensity (see examples in Majer 1983). Species richness values ranged from 5-15 in the replaced ecosystems, which is beneath the range exhibited by all but one of the undisturbed sites. The range and number of total genera was similar in the undisturbed and the modified groups of sites, being 10-15 and 9-14 respectively. There was, however, a discontinuity in the range of values for the replaced group of sites, where values ranged from 4-10. The ratio of species/genera reflected these trends, and ranges respectively varied from 1.50-2.08, 1.43-1.78 and 1.20-1.50 for the undisturbed, modified and replaced groups of sites.

Evenness values varied greatly between sites, often in cases where the vegetation was of the same type. This can result from the placing of traps near nests or ant trails, and highlights one of the problems of using this community index for ants. Most values for the undisturbed and modified sites fell within the range of 0.60-1.00, which is typical of native vegetation in Western Australia (Majer 1983). However, two of the undisturbed sites (Jarrah woodland J2 and Tuart woodland T1) exhibited exceptionally low values, as did the *Eucalyptus* plantations (EP1 and EP2) and one of the pine plantations (P1). It is interesting that gardens exhibited relatively high evenness values.

Functional groups

The distribution of ant species in functional groups is shown in Fig 2. This figure expresses the data as total ant species obtained by all sampling methods (Fig 2A) and as the proportion of individuals in the pitfall trap catch (Fig 2B). The latter analysis does not represent as many species as the former, because not all species were sampled by the pitfall traps.

Although all seven functional groups were present in at least some of the undisturbed and modified sites (Fig 2A), they were not present in all of them. This was because large, solitary foragers were not encountered at some sites and the disturbed tuart site TD lacked both large, solitary foragers and also dominant *Iridomyrmex* species. The numbers of functional groups in the modified sites vary within the range shown by the undisturbed sites. However, numbers of functional groups were lower in some of the replaced sites such as garden site G1, both *Eucalyptus* plantations and particularly in the pine plantations which lacked large, solitary foragers, cryptic species, subordinate species and, in the case of P1, dominant *Iridomyrmex* species.

The relative contribution of ant individuals to the various functional groups varied greatly between the

various undisturbed and modified sites (Fig 2B) and no generalizations may be made, except that the ant communities at these sites were well represented by individuals from all functional groups except the large solitary foragers. This in part may be influenced by the inefficiency of the pitfall traps for catching large ants. By contrast, the catches in the *Eucalyptus* plantation and one garden (G2) were disproportionately comprised of dominant *Iridomyrmex* species and the pine plantations by opportunistic species.

Multivariate analyses

Examination of the dendrogram which classifies sites on the basis of ant species composition revealed that two major groups of sites could be discerned, each containing three sub-groups. These six sub-groups are superimposed on Fig 3. The first major group contained all modified and replaced sites, plus site T2 (tuart). The second major group contained only undisturbed sites. Within the first major group (containing modified and replaced sites), the first sub-group contained site T2 (a moist tuart site), the two Boomerang Gorge sites (BG1 and BG2), the disturbed tuart site (TD) and a disturbed tuart/heath site (HD), while the second contained the two garden sites (G1 and G2) and the eucalypt plantation sites (EP1 and EP2) and the third contained the two pine sites (P1 and P2). Within the second major group (undisturbed sites), the first sub-group contained a *Banksia* woodland site (B1), two jarrah woodland sites (J1 and J2) and a *Dryandra* heath (D1), the second contained a *Dryandra* heath (D2) and a dry tuart site (T1),

Table 2

Number of species of ants within each genus and various other summary data for the ant communities sampled within disturbed and undisturbed plots in and near Yanchep National Park.

	Quindalup heath		Dryandra heath		Banksia woodland		Jarrah woodland		Tuart woodland		Dist. heath	Disturbed tuart			Gardens		Eucalyptus plantation		Pine plantation	
	Q_1	Q_2	D_1	D_2	B_1	B_2	J_1	J_2	T_1	T_2	HD	TD	BG_1	BG_2	G_1	G_2	EP_1	EP_2	P_1	P_2
Myrmeciinae																				
Myrmecia			1				2	1	1	1	1			1		1				
Ponerinae																				
Brachyponera	1						1	1			1									
Cerapachys		1					1													
Heteropouera										1										
Hypoponera															1					
Platythyrea																				
Rhytidoponera			1	1	2	1	3	2	2	2	1	2	1	2	2	2	1	1	1	1
Trachymesopus																1				
Myrmicinae																				
Adlerzia									1											
Anisopheidole								1				1					1			
Aphaenogaster	1	1	1				1	1									1	1		
Cardiocondyla															1	1	1	1		
Crematogaster	3		3	2	1	2	1	2	2	1	1	1	1	1	1	1				
Meranoplus	1	1	2		1		1	1	1	1										
Monomorium	2	6	4	2	3	2	1	2	3	4	2	4	3	1	2		2	1	2	1
Pheidole	1	1	1			1			1	1	1	1	1	1		1	1	1	1	1
Podomyrma		1	1										1							
Solenopsis								1							1	1	1			
Strumigenys														1						
Tetramorium			1		2		1	1		1	1		1		1	1	1	1		
Dolichoderinae																				
Dolichoderus					1		1	1	2	2	1	1	2	1						
Iridomyrmex	4	6	6	1	4	4	4	5	4	3	4		3	4	4	3	3	3		2
Tapinoma	2	1	1	1			1									1				
Formicinae																				
Campouotus	3	3		1	1	2	2	2	5		4	1	2	2		1	1	2		
Melophorus	2	2	4	3	4	1	6	3	4	1	2	2	4	2	1		2	2	1	
Notoncus	1	1	1			1			1	1	1		1	1						1
Paratrechina															1					
Plagiolepis							1		1	1					1					
Polyrhachis				1																
Prolasius				1					1	1						1				
Stigmacros	1	1	1	1	1		2	1				3	1	1						
Total species	22	25	27	15	20	18	28	23	27	21	22	16	23	20	15	13	14	13	5	6
Total genera	12	12	13	11	10	12	15	13	12	14	14	9	14	14	10	10	10	9	4	5
Species/genera	1.83	2.08	2.08	1.36	2.00	1.50	1.87	1.77	2.25	1.50	1.57	1.78	1.64	1.43	1.50	1.30	1.40	1.44	1.25	1.20
Evenness index (J')	1.03	0.87	0.82	0.67	0.49	0.70	0.68	0.32	0.24	0.58	0.84	0.63	0.58	0.91	0.67	0.67	0.37	0.49	0.44	0.67
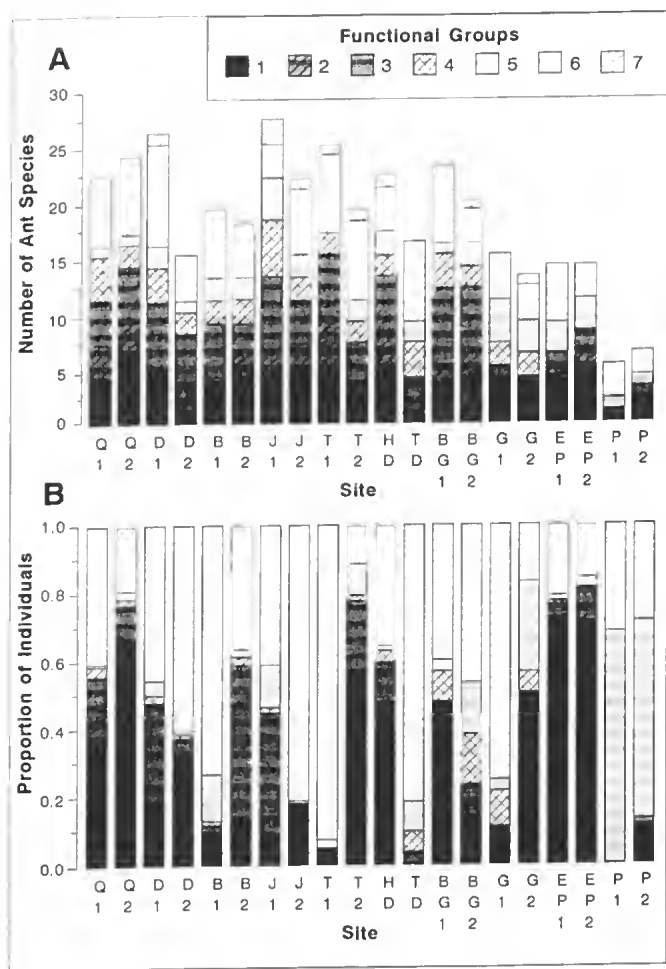
Figure 2. Breakdown of ant species by functional groups (after Greenslade & Thompson 1981 and Andersen 1987, 1990) in terms of (**A**) total ant species obtained by all sampling methods and (**B**) proportion of ant individuals in the pitfall trap catch. Key to functional groups: 1, dominant species; 2, subordinate species; 3, climate specialists; 4, cryptic species; 5, opportunists; 6, generalized myrmicines; 7, large solitary foragers.

and the third contained a site with open *Banksia* woodland over heath (B2) and two heath sites on Quindalup dunes (Q1 and Q2).

The groups identified from the output of the classification analysis could also be discerned in the scattergrams from the ordination of sites in terms of their ant species composition (summarized in Fig 3). Following rotation of the ordination output (see Belbin 1989), about 44% of the variance accounted for in the three dimensional ordination (stress = 0.16) was due to factors influencing axis 2, with 29% influencing axis 1 and 27% influencing axis 3. It is apparent that disturbed sites were mostly differentiated from undisturbed ones on the second axis. Groups appearing close together on Fig 3 are fairly well separated on the third axis: for example, sites T2, G1 and D2.

Four groups of species were chosen from the classification of ant species on the basis of the sites at which they occurred. The dendrogram was limited to four groups as this was the largest number that could be interpreted ecologically in terms of habitat usage by individual species. The first group contained species such as *Crematogaster* sp JDM 33 (that is, conspecific with *Crematogaster* sp JDM collection 33), *Tapinoma* sp JDM 134 and *Iridomyrmex* sp 18

(ANIC) (that is, conspecific with *Iridomyrmex* sp 18 Australian National Insect Collection [ANIC]) which are more frequent in, or confined to, undisturbed native vegetation. Patchily distributed species such as *Camponotus* sp 22 and *Camponotus* sp 36, which were less frequent in disturbed sites, were characteristic of groups two and three. The fourth group contained two subgroups. The first subgroup included widespread, frequently occurring species such as *Iridomyrmex agilis* gp 21 (ANIC), *Monomorium* sp JDM 225 and *Rhytidoponera violacea*. The second sub-group included species such as *Melophorus* sp 2 (ANIC) and *Tetramorium bicarinatum*, which are restricted to, or more frequent in, disturbed or moist sites.

Comparison with vertebrate species richness

In the undisturbed sites, the number of species of ants varied from 18 to 27, reptiles and amphibians from eight to 15, birds from 17 to 35 and mammals from two to six; total numbers of vertebrate species varied from 24 to 47 (Table 3). There was no significant correlation between ant species richness and vertebrate species richness. The Spearman rank correlation coefficients were: reptiles - 0.18, birds 0.30, mammals - 0.01 and for all vertebrates combined 0.25.

Discussion

Much of the native vegetation at Yanchep National Park supports ant communities which, in terms of species richness, evenness and functional group profiles, are typical of undisturbed environments elsewhere which have been sampled at this intensity (data in Andersen 1987, 1990, Majer 1983). Indeed, the composition of the ant fauna in the undisturbed sites is similar to that reported for equivalent locations on the Swan Coastal Plain by Rossbach & Majer (1983).
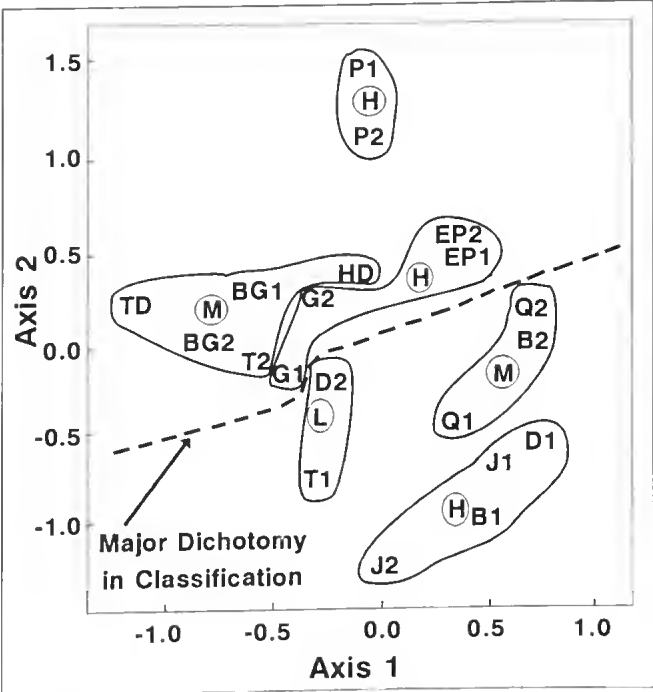
Figure 3. Results of the classification of sites in terms of ant species occurrences, superimposed on the first two axes of the ordination plot. The continuous lines encompass the members of each of the six subgroups recognized in the classification analysis. L, M and H denote low, medium and high values respectively on the third axis of the ordination.

Table 3

Species richness of ants and vertebrates at ten undisturbed sites in Yanchep National Park. (Vertebrate data from A H Burbidge & J K Rolfe unpublished).

Site	Species richness				
	Ants	Reptiles and amphibians	Birds	Mammals	Total vertebrates
Q1	22	11	26	6	43
Q2	25	11	26	6	43
D1	27	9	16	6	31
D2	15	8	12	4	24
B1	20	12	25	5	42
B2	18	15	17	6	38
J1	28	9	30	2	41
J2	23	11	25	5	41
T1	27	10	23	5	38
T2	21	8	35	4	47

The findings of the present survey also indicate that the ant fauna is altered by even slight modifications of the ecosystem, such as by trampling, exotic plant and weed invasion (for example plots BG1 and BG2) or by partial clearing followed by natural regrowth (for example plots HD and TD). The ant fauna in these modified ecosystems has a characteristic species composition and also slightly reduced species richness. The range of genera and the representation of ants in the major functional groups still lies within the range exhibited by the undisturbed sites, indicating that the main elements of the fauna are still present even though the species composition is changed.

The ecosystems in which the native vegetation has been replaced by a new one, such as a garden, or eucalypt or pine plantation, exhibited the most altered ant communities. Species and generic richness is considerably reduced, fewer functional groups are represented and, especially in the case of the pine plantations, the composition of species present is very different from that in the undisturbed areas. Evenness values (Table 2) were also atypical, but in some areas they are exceptionally low (EP1, EP2 and P1) while in the gardens they are relatively high. This is consistent with the fact that the plantations are dominated by one or a few species whereas the gardens support a wider range of species, none of which dominate the area. Presumably the ant fauna tends to reflect the distribution of plant species or their associated structural attributes within each plot.

The more disturbed the site, the fewer ant functional groups were present (Figures 2A and B). Cryptic species may have been lost due to disturbance of the litter layer; litter of native plants may be replaced by dried grass or bare patches. Some of the large, solitary foragers and sub-ordinate species may be specialists which are unable to withstand the changed environment. Also, the dominant *Iridomyrmex* group may be absent from one of the pine plantations because of the heavy shade, a condition which does not favour this sun-loving genus, or alternatively due to the lack of invertebrate food resources in pine litter (Springett 1971).

The changes in the functional group profiles are also reflected in the presence or absence of particular ant species. The elucidation of indicator ant species, whose presence or absence indicates a particular environmental condition, is confounded by the fact that some species are rare and hence not commonly sampled. The absence of such species in a sample could therefore result from

under-sampling or from a genuine absence of the species. With this limitation in mind, it appears that the presence of *Crematogaster* sp JDM 33, *Tapinoma* sp JDM 134 and *Iridomyrmex* sp 18 (ANIC) are indicative of sites in the relatively undisturbed state. Reasons for their presence could include respectively the presence of tree-nesting/foraging sites (*Crematogaster* sp JDM 33), a dense litter layer (*Tapinoma* sp JDM 134) and a mosaic of insolated ground, for nesting, together with a vigorous native herb and shrub layer which supports nectar and prey items (*Iridomyrmex* sp 18 (ANIC)). By contrast, *Melophorus* sp 2 (ANIC) and *Tetramorium bicarinatum* appear to be indicative of highly disturbed environments and may be benefiting from the highly insolated ground in cleared areas and from the abundance of grass seeds on which they feed.

The ant component of the fauna at Yanchep National Park is vulnerable to disturbance. The fact that changes in the ant fauna go hand in hand with changes in the composition of other invertebrates (Majer 1983) suggests that many other invertebrate groups would also be influenced by these disturbances. The ant data are less likely, however, to provide useful information concerning vertebrate species. At undisturbed sites, we found no significant correlation between the levels of species richness for ants and species richness of any major vertebrate groups or for all vertebrates combined. Ants (and presumably other invertebrates) show quite different patterns of occurrence than do vertebrates at Yanchep National Park.

From a conservation management point of view, it is important to have data concerning, and an understanding of, both vertebrate and invertebrate communities. Yanchep National Park has been subjected to various pressures including weed invasion, trampling, clearing of land around facilities, altered fire regimes and grazing (historically by domestic stock, currently by kangaroos and introduced rabbits). The observed sensitivity of the ant fauna to disturbance (including modification of vegetation structure) highlights the need to manage the area in such a way that such impacts are minimized; in view of the observed correlation between the species richness of ants and many other invertebrate taxa (Majer 1983) this would also be expected to minimize the effects on most other invertebrate groups. Information on vertebrates and vascular plants (A H Burbidge *et al.* unpublished) which is currently being analysed, will complement the ant study. When complete, these studies should provide guidelines for managing the park to ensure that biodiversity is not adversely affected by the usage and management regimes to which it is subjected.

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Recent Advances in Science in Western Australia

Life Sciences

House mice have been shown by C R Dickman of the University of Sydney to respond to odours of their predators. Mice in areas with few endemic predators (cats, foxes, native cats) poorly discriminate between traps with and without faecal odours of the predators and do not prefer dense vegetation, whereas mice in areas with predators avoid traps with predator faecal odours and prefer dense vegetation. The survival rate for predator-experienced mice introduced to a study area containing cats and foxes is $2^{1}/_{2}$ times higher than for predator-naive mice:

> Dickman C R 1992 Predation and habitat shift in the house mouse, *Mus domesticus*. Ecology 73:313-322.

The standard metabolic rate of two species of varanid lizard has been shown by researchers from the University of Western Australia and Edith Cowan University to be proportional to body mass, rather than the more general relationship for animals of body mass$^{0.75}$. There was an exponential effect of ambient temperature on standard metabolic rate, and no plateau was observed for SMR between 30 and 40°C:

> Thompson G G & Withers P C 1992 Effects of body mass and temperature on standard metabolic rates for two Australian varanid lizards (*Varanus gouldii* and *V. panoptes*). Copeia 1992:343-350.

Postmating mortality was thought to occur only in male *Antechinus* and *Phascogale* dasyurids, but C R Dickman of the University of Sydney and R W Braithwaite of the Division of Wildlife & Ecology, CSIRO Winnellie, report for the first time postmating mortality in field populations of the Dibbler (*Parantechinus apicalis*) and the native cat (*Dasyurus hallucatus*). The variation in life history strategies of dasyurids is more pronounced than had been suspected:

> Dickman C R & Braithwaite R W 1992 Postmating mortality of males in the dasyurid marsupials, *Dasyurus* and *Parantechinus*. Journal of Mammalogy 73:143-147.

The honey possum is a small (7-15 g) nectar-feeding marsupial found only in south-western Australia. Although females have four teats, they rarely rear four young to independence. R D Wooller and K C Richardson of Murdoch University have demonstrated that most honey possums have a progressive reduction in the number of offspring as they grow in the pouch. This progressive brood reduction may optimise offspring production during the short lifetime of honey possums, in response to an unpredictable and specialised food supply:

> Wooller R D & Richardson K C 1992 Reduction in the number of young during pouch life in a small marsupial. Journal of Zoology, London 226:445-454.

Researchers from the University of Western Australia have found a negative relationship between home range size and natural food abundance for a population of the southern brown bandicoot. However, home range area was found to increase with the provision of supplementary food. Bandicoots were not territorial, and the flexibility of their home range allows opportunistic exploitation of resources:

> Broughton S K & Dickman C R 1992 The effect of supplementary food on home range of the southern brown bandicoot, *Isoodon obesulus* (Marsupialia: Peramelidae). Australian Journal of Ecology 16:71-78.

Ritual combat has been reported between males of a variety of varanid lizards, but G G Thompson and P C Withers of the University of Western Australia and Edith Cowan University report for the first time male ritual combat for *Varanus caudolineatus* and *V. gouldii*. Behavioural variation in male ritual combat for these species is consistent with descriptions for other species in different *Varanus* lineages:

> Thompson G G & Withers P C 1992 The combat ritual of two monitor lizards, *Varanus caudolineatus* and *Varanus gouldii*. West. Aust. Naturalist 19:21-25.

Earth Sciences

Landform and regolith stratigraphy for ten localities in Western Australia are used by D K Glassford and V Semeniuk to demonstrate that the Cainozoic cover predominantly consists of granitic saprolite unconformably overlain by allochthonous deposits which are mainly altered aeolian sands and sandy dusts. These descriptions challenge the traditional views of the autochthonous and colluvial origin of the Cainozoic cover of SW Australia:

> Glassford D K & Semeniuk V 1991 Arid-zone landforms and Cainozoic regolith of the Yilgarn Block region of Western Australia. Excursion Guidebook, Joint Conference on Desert Landscapes and Past and Future Evolution of Deserts, International Geological Correlation Program Project 252. Bullcreek, Western Australia.

R W Young of the University of Wollongong provides an interesting contribution to geomorphological debate on the survival of features of great antiquity. The modern landscape of the East Kimberley bears the imprint of geological constraints (continental rifting, basin geometry and depositional style, variable digenesis and relict weathering). The broad outline of the topography is interpreted as a Gondwanan relict, with only the final phase being post-Miocene:

> Young R W 1992 Structural heritage and planation in the evolution of landforms in the East Kimberley. Australian Journal of Earth Sciences 39:141-151.

Researchers from the Geological Survey of Western Australia and Curtin University examine late Archaean plate tectonics using Rb-Sr, Sm-Nd and REE characteristics of granitic rocks. Granite-greenstones in the south-eastern Pilbara Craton are different from northern Pilbara granite-greenstones. A shear zone separating the Mosquito Creek Synclinorium from the Kurrana Batholith has characteristics of a suture zone, and is postulated to be the boundary between two distinct terrains that joined to form the Pilbara Craton between 3.0 and 2.76 Ga:

> Tyler I M, Fletcher I R, de Laeter J R, Williams I R & Libby W G 1992 Isotope and rare earth element evidence for a late Archaean terrane boundary in the southeastern Pilbara Craton, Western Australia. Precambrian Research 54:211-229.

A comprehensive overview of the Darling Range as the world's leading bauxite producing region (16% of total world production) is provided by researchers from the Geological Survey of Western Australia. The lenticular

alumina-rich ore bodies, in the lateritic upland geomorphological division of the Darling Plateau, each contain 10 to 25 Mt, and the total economic bauxite resource is estimated at over 3500 M:

Hickman A H, Smurthwaite A J, Brown I M & Davy R C 1992 Bauxite mineralization in the Darling Range, Western Australia. Western Australia Geological Survey Report 33.

Note from the Hon Editor: This column helps to link the various disciplines and inform others of the broad spectrum of achievements of WA scientists (or others writing about WA). Contributions to "Recent Advances in Science in Western Australia" are welcome, and may include papers that have caught your attention or that you believe may interest other scientists in Western Australia and abroad. Papers in refereed journals, or books, chapters and reviews will be accepted. Abstracts from conference proceedings will not be accepted. Please submit short (2-3 sentence) summaries of recent papers, together with a copy of the title, abstract and authors' names and addresses, to the Hon Editor or a member of the Publications Committee: Dr S D Hopper (Life Sciences), Dr A E Cockbain (Earth Sciences), and Assoc Prof J Webb (Physical Sciences). Final choice of articles is at the discretion of the Hon Editor.

"Letters to the Editor" concerning scientific issues of relevance to this journal are also published at the discretion of the Hon Editor. Please submit a word processing disk with letters and suggest potential reviewers or respondents to your letter.

P C Withers, Hon Editor, Journal of the Royal Society of WA.

Errata

Alphabetic letters with diacritical marks were inadvertently not printed in Volume 75 Part 3, but were replaced by a space. The correct authority names for species were:

Kyphosus sydneyanus Günther (page 67)

Lupinus digitalis Forskål (title page, pages 83-88)

The correct journal name for the reference, Tuschnjakowa (1935), on page 88 was:

Der Züchter

The micro-Crustacea and physico-chemical features of temporary ponds near Northcliffe, Western Australia

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Abstract

Thirty five micro-crustacean species were recorded in seven temporary ponds located between Northcliffe and Windy Harbour, Western Australia, sampled in 1977, 1980 and 1990. Three physico-chemical parameters were determined for seven ponds in 1977 and six parameters for four ponds in 1980. Ponds varied in acidity, but high acidity did not lower species richness; one pond with a pH of 4.2-4.5 had the highest mean species richness. Species endemic either to the Northcliffe region or to south-western Australia are *Daphnia occidentalis, Calamoecia elongata, C. attenuata, Boeckella geniculata, Hemiboeckella andersonae, Paracyclops* sp. nov. and *Biapertura imitatoria*. The following species are regarded *pro tem* as being acidophilic: *D. occidentalis, C. elongata, P.* sp.nov., *B. imitatoria, B. longinqua, Monope reticulata* and *Rak obtusus. Hemiboeckella searli* and *Metacyclops* sp. (cf. *arnaudi*) appear early in succession. *H. andersonae* may also appear early, or may be delayed. Unlike the fauna of lotic environments in the study region, there are presently no sound data for concluding that the micro-crustacean fauna of lentic environments is impoverished relative to that in south-eastern Australia.

Introduction

The moist south-west corner of Western Australia is of outstanding interest from the viewpoint of both phytogeography (Hopper 1979, Nelson 1981) and zoogeography (Kikkawa *et al.* 1979). With respect to the freshwater fauna, there is a high degree of endemism in Western Australia (Maly & Bayly 1991, Frey 1991), and a high proportion of these endemics occur in, or are restricted to, the far south-west of that State.

Although various freshwater taxa occurring in this region have received attention by taxonomic specialists, more comprehensive studies of fresh waters in the Northcliffe-Walpole region commenced only recently. Bayly (1982) published a brief account of the ecology of temporary pools on granite outcrops in southern Western Australia, including six small pools located within a 15 km radius of Northcliffe, each of which was sampled three times during the winter of 1977. Pusey & Edward (1990) studied the invertebrate ecology of nine sites including two temporary pools which are in the same region as the seven ponds discussed in the present study.

The present study overlaps in a temporal sense with that of Bayly (1982) but excludes water bodies lying directly on granite rock substrata. The study had two main aims: to establish for zoogeographic purposes the precise nature of the micro-crustacean fauna of the temporary waters, and to examine some general aspects of the ecology of the waters that are highly distinctive in a chemical sense.

Study Area

The study area (Fig 1) is located in the mesic far south-west corner of Western Australia where the summers are dry and the winters are wet.

Rainfall data for Pemberton for the 1977 sampling period are presented in Fig 2A; the three sampling dates occurred 19, 33 and 47 days after the break of the wet season (16 May). Rainfall data relevant to the 1980 sampling are given in Fig 2B; the break occurred on 17 April and the first sampling did not occur until 49 days later.

The location of the ponds is shown in Fig 1. Ponds 1 and 2 were located 2.3 km (by road) south of Northcliffe on formerly forested land which had been cleared and put into pasture. These two ponds were scarcely separated from each other and with high rainfall would become confluent. Both of these ponds had well developed macrophyte beds in which *Callitriche* L. was dominant and *Cotula coronopifolia* L. also occurred. Pond 3 (6.0 km south of Northcliffe) lay on, and was surrounded by, natural swamp land with large clumps of *Juncus* L. but the water had probably been impounded by road construction. It contained dark, humic water and extensive beds of macrophytes dominated by *Triglochin* L. Pond 4 (6.7km south of Northcliffe) was a large ditch which had been excavated during road-making activities. It was sufficiently old to have become colonised by clumps of *Juncus*. Locality 5 (7.1 km south of Northcliffe) was a small, shallow roadside pool that entirely lacked macrophytes. Ponds 6 and 7 (10.8 km south of Northcliffe and 1.1 km south of Mt Chudalup, respectively) were in open coastal heath and sedgelands. Both had sandy bottoms and contained dark, humic water and few, if any, macrophytes.

Methods

Biological aspects

Each pond was thoroughly sampled with the zooplankton net described by Bayly (1982). Sampling was restricted to June and early July. In 1977, each pond was sampled three times at fortnightly intervals. In 1980, ponds 1-4 were sampled eight times at 2-4 day intervals. In 1990, ponds 1-4 were sampled once only—on 1 July.
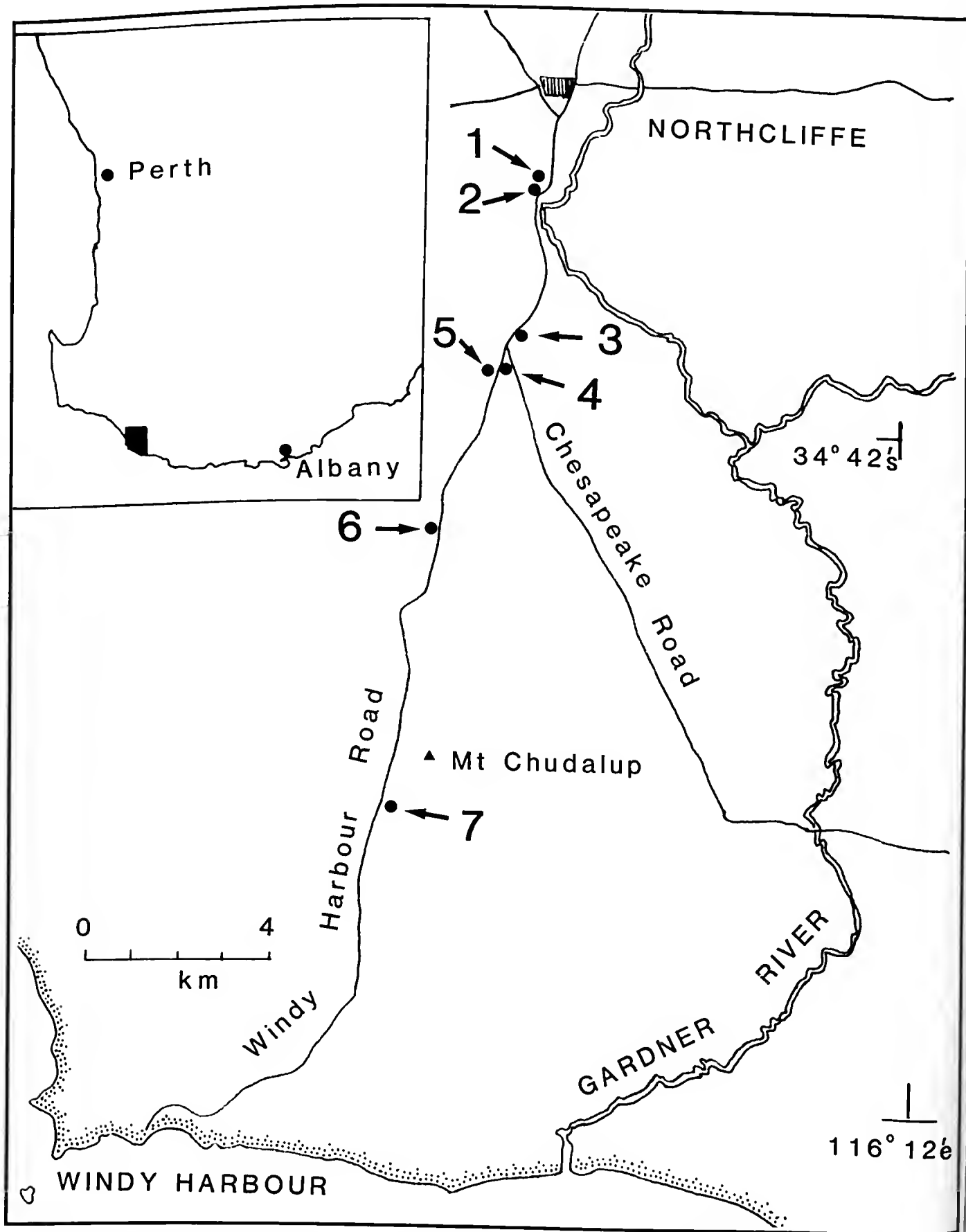
Figure 1 Map showing the study area in south-west Western Australia and the location of the seven ponds studied.
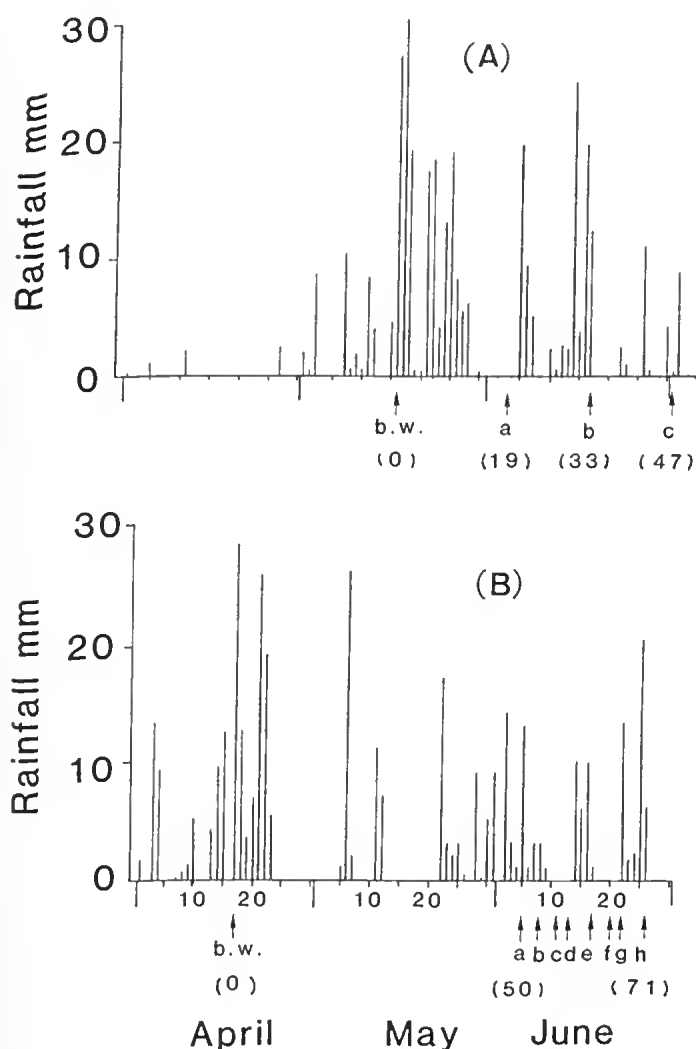
Figure 2 Rainfall recorded at Pemberton (near Northcliffe) from 1 April-30 June, A in 1977, and B in 1980. Break of the wet season (b.w.) occurred on 16 May 1977 and 17 April 1980. Number of days that elapsed after the break is given in parentheses below each of the three sampling days (a = 3 June, b = 17 June and c = 1 July) in 1977, and for the first and last of the eight sampling days (a = 5 June, b = 8 June, c = 11 June, d = 13 June, e = 17 June, f = 20 June, g = 23 June, h = 26 June) in 1980.

In the laboratory, collections were studied and sorted under a stereo-microscope. In 1977, the calanoid copepod species were subject to ordinal level of measurement and, for this reason, numbers (showing the order of abundance with the most abundant being 1) appear for them in Tables 3-7. Otherwise, the presence only (nominal level of measurement) of various taxa was recorded (indicated by the symbol X in Tables 3-7).

It was not possible to identify cyclopoid copepods and ostracods in all of the large number of samples taken during 1980; full identifications were obtained for the first series of samples taken on 5 June and also for those taken on 23 June. For other sampling dates in 1980 (except for cyclopoids at locality 1), the presence of cyclopoids and ostracods was recorded without further taxonomic resolution (see Tables 3-7). Detailed identifications of cyclopoids occurring at locality 1 were obtained for all of the 1980 collections.

Physico-chemical aspects

In 1977, three parameters (temperature, conductivity and pH) were measured using the methods described by Bayly (1982). In 1980, five parameters were measured: temperature, dissolved oxygen and REDOX potential were measured with a "Hydrolab 8000" (Hydrolab Corp., Texas) integrated, multiparameter instrument, while conductivity and pH were measured as in 1977.

In both 1977 and 1980 the depth of each pond was measured with the device described by Bayly (1982).

Results

Physico-chemical aspects

Results for 1977 are given in Table 1. Except for 3 June at locality 1, conductivities (K_{18}) were no greater than 270 μS cm^{-1}. All of the five localities at which pH measurements were made were acidic; localities 3 and 6 were strongly acidic. Daytime temperatures lay in the range 10.5-19.8°C. None of the ponds was deeper than 72 cm.

Table 1
Physico-chemical features of Northcliffe-Windy Harbour ponds in 1977

Locality number	Date	Maximum depth (cm)	Conductivity (K_{18}) (μS cm^{-1})	pH	Temperature (°C)
1	3 June	14	508		19.2
	17 June	38	167		14.9
	1 July	40	223		16.5
2	3 June	14	139		19.8
	17 June	39	129	6.2	14.4
	1 July	40	126		15.5
3	3 June	37	215		10.9
	17 June	50	185		12.4
	1 July	58	180	4.2	11.8
4	17 June	72	54		13.2
	1 July	60	71	5.1	13.1
5	3 June	24	77		12.7
	17 June	31	117	5.7	14.3
	1 July	32	142	5.6	10.5
6	3 June	25	234		14.3
	17 June	40	267	4.0	14.2
	1 July	40	270		10.6
7	3 June	45	169		17.4
	17 June	55	190		14.0
	1 July	56	251		12.1

Results for 1980 are presented in Table 2. Conductivity results were concordant with those obtained in 1977, the mean order for the locality numbers being 1>3>2>4. The pH of localities 1 and 2 was closely similar and remained fairly constant at about 6.0. Localities 3 and 4 were closely similar and highly acidic; pH lay in the range 4.2-4.6. For both dissolved oxygen and REDOX potential the mean values for the four localities showed the same order: 4>3>2>1. Water temperatures lay in the range 7.5-13.3°C. The maximum depth of all ponds showed a tendency to increase during the sampling period.

Biological aspects

The occurrence of micro-crustacean taxa in 1977, 1980 and 1990 is shown in Tables 3-7. A total of 35 taxa were recorded during this study.

Table 2

Physico-chemical features of Northcliffe-Windy Harbour ponds in winter of 1980. Except for maximum depth, the values given are means ± standard errors for 8 sampling days.

Locality number	Maximum depth (cm)[1]	Conductivity (K_{18}) $(\mu S\ cm^{-1})$	pH	Temperature (°C)	REDOX potential (mV)	Dissolved oxygen $(mg\ l^{-1})$
1	34-43	269±21	6.04±0.03	10.7±0.5	253±12	4.1±0.6
2	22-46	159±2	5.83±0.04	11.1±0.5	287±9	6.2±0.4
3	32-49	223±4	4.33±0.03	10.1±0.6	351±8	6.5±0.3
4	65-75	69±2	4.45±0.02	11.1±0.5	377±6	8.1±0.1

[1]The lower value of the range corresponds with the depth found on 5 June and the higher value corresponds with the depth recorded on 26 June.

Table 3

Northcliffe locality one. Occurrence of micro-crustacean taxa in samples taken on various dates in 1977, 1980 and 1990. The presence of taxa is indicated by "X" for mature individuals or "J" where only juvenile individuals were present. The relative abundance of Calanoida is indicated by 1 (most abundant) or 2 (less abundant).

TAXA	1977			1980								1990
	3 June	17 June	1 July	5 June	8 June	11 June	13 June	17 June	20 June	23 June	26 June	1 July
CALANOIDA				J	J	J	J					
Calamoecia attenuata Fairbridge			2									
Hemiboeckella andersonae Bayly		1	1						X	X	X	X
CYCLOPOIDA												
Austrocyclops australis (Sars)							X					X
Mesocyclops sp.			X	X					X		X	X
Metacyclops sp. (cf. *arnaudi*)				X	X	X			X			
OSTRACODA				X	X	X	X	X			X	
Bennelongia australis (Brady)	J	J	X							J		J
Cypretta viridis (Thompson)	J		X							J		X
Eucypris virens (Jurine)		X		J						X		
CLADOCERA												
Biapertura cf *macrocopa* (Sars)			X							X	X	
Ceriodaphnia sp.												X
Chydorus cf *sphaericus* (O.F.Muller)	X	X	X	X	X	X	X	X	X	X	X	X
Pleuroxus inermis Sars	X	X	X	X		X						X

Table 4

Northcliffe locality two. Occurrence of micro-crustacean taxa in samples taken on various dates in 1977, 1980 and 1990. The presence of taxa is indicated by "X" for mature individuals or "J" where only juvenile individuals were present. The relative abundance of Calanoida is indicated by 1 (most abundant) or 2 (less abundant).

TAXA	1977			1980								1990
	3 June	17 June	1 July	5 June	8 June	11 June	13 June	17 June	20 June	23 June	26 June	1 July
CALANOIDA												
Calamoecia attenuata Fairbridge	—	1	1	X	X	X	X	X	X	X	X	
Hemiboeckella andersonae Bayly	—	2	2	X	X	X	X	X	X	X	—	
CYCLOPOIDA				X	X	X	X	X			X	
Austrocyclops australis (Sars)	—	X	X	X								X
Mesocyclops sp.	—	X	X	X								X
Metacyclops sp. (cf *arnaudi*)				X						X		
OSTRACODA				X	X	X	X	X			X	
Bennelongia australis (Brady)	J	J	X									X
Cypretta viridis (Thomson)	J	X	X	X						X		X
Eucypris virens (Jurine)		X		X						X		
CLADOCERA												
Biapertura cf *macrocopa* (Sars)	—	—	X	—	—	—	—	—	X	X		
Chydorus cf *sphaericus* (O.F.Muller)	X	X	X	X	X	X	X	X	X	X	X	X
Daphnia sp.												X
Pleuroxus inermis Sars	X	X	X									X
Simocephalus sp.												

Table 5

Northcliffe locality three. Occurrence of micro-crustacean taxa in samples taken on various dates in 1977, 1980 and 1990. The presence of taxa is indicated by "X" for mature individuals or "J" where only juvenile individuals were present. The relative abundance of Calanoida is indicated by 1 (most abundant) to 3 (least abundant).

TAXA	1977			1980								1990
	3 June	17 June	1 July	5 June	8 June	11 June	13 June	17 June	20 June	23 June	26 June	1 July
CALANOIDA												
Calamoecia attenuata Fairbridge	—	1	2	X	X	X	X	X	X	X	X	X
C. elongata Bayly	—	2	1	X	X	X	X	X	X	X	X	X
Hemiboeckella searli Sars	J[1]	3	3	X	X	X	X	X	X	X	X	X
CYCLOPOIDA					X	X	X	X	X		X	
Mesocyclops sp.	X	X	—	X								
Paracyclops sp nov	—	X	X							X		X
Macrocyclops albidus (Jurine)												X
CLADOCERA												
Alona sp. nov.	X	—	—	X	X	X	X	X	X	X	X	
Alonella cf *excisa* (Fisher)	X	X	X	X	X	X	X	X	X	X	X	X
Biapertura cf *macrocopa* (Sars)	—	X	—	X	X	X	X	X	X	X	—	
B. longinqua Smirnov				X	X	X	X	X	X	—	X	
Camptocercus sp.				X	X	—	X	X	—	X	—	
Daphnia occidentalis Benzie	X	X	X	X	X	X	X	X	X	X	X	X
Graptoleberis sp.				X	X	X	X	X	X	X	—	
Monope reticulata (Henry)				—	X	—	—	—	X	X	—	
Scapholeberis kingi Sars	X	X	X	X	X	X	X	X	X	X	—	

[1]None mature, but copepodite stage V present and positively identifiable from the very unequal length of the furcal setae (see Bayly 1974, P.92).

Table 6

Northcliffe locality four. Occurrence of micro-crustacean taxa in samples taken on various dates in 1977, 1980 and 1990. The presence of taxa is indicated by "X". The relative abundance of Calanoida is indicated by 1 (most abundant) to 3 (least abundant).

TAXA	1977		1980								1990
	17 June	1 July	5 June	8 June	11 June	13 June	17 June	20 June	23 June	26 June	1 July
CALANOIDA											
Boeckella geniculata Bayly	2	3	X	X	X	X	X	X	X	X	
Calamoecia attenuata Fairbridge	1=	2	X	X	X	X	X	X	X	X	X
C. elongata Bayly	1=	1	X	X	X	X	X	X	X	X	X
CLADOCERA											
Alonella cf *excisa* (Fisher)	X	X	—	—	X	X	X	X	X	X	X
Biapertura cf *macrocopa* (Sars)	X	—	—	—	—	—	X	—	X	X	
Monope reticulata (Henry)	X	—	—	—	—	—	X	—	—	—	
Scapholeberis kingi Sars			X	X	X	X	X	X	X	—	

In 1977, and omitting locality 4 which was not sampled on 3 June, the mean number of species per locality increased with time (3 June, 4.5 species; 17 June, 6.5 species; 1 July, 7.3 species) and the total number of species recorded per locality varied as follows: locality 1 (9 species), 2 (10 spp), 3 (10 spp), 4 (6 spp), 5 (8 spp), 6 (11 spp) and 7 (9 spp).

In 1980, the total number of species recorded from the various localities was as follows: locality 1 (10 species), 2 (9 spp), 3 (14 spp) and 4 (7 spp).

On 1 July 1990 the mean number of species per locality (localities 1-4) was 6.3. The total number of species was as follows: 1 (8 spp), 2 (7 spp), 3 (7 spp) and 4 (3 spp).

Discussion

There are two themes of particular interest associated with the limnology of the Northcliffe region: endemism and peculiar water chemistry. This study provides a basis on which to compare micro-crustacean colonization of acidic ponds in Western Australia, other parts of Australia, and in other countries.

Maly & Bayly (1991) and Frey (1991) have emphasised that many of the microcrustacean taxa in Western Australia do not occur in eastern Australia. Epicontinental seas covered much of Australia during part of the Early Cretaceous (ca. 120-110 Ma BP) and the western half of

Table 7

Northcliffe localities five, six and seven. Occurrence of micro-crustacean taxa in samples taken on various dates in 1977. The presence of taxa is indicated by "X" for mature individuals or "J" where only juvenile individuals were present. The relative abundance of Calanoida is indicated by 1 (most abundant) to 4 (least abundant).

LOCALITY NUMBER	5			6			7		
TAXA	3 June	17 June	1 July	3 June	17 June	1 July	3 June	17 June	1 July
CALANOIDA									
Calamoecia elongata Bayly	J	X	X						
C. tasmanica[1]					1	2	1	1	1
Hemiboeckella andersonae Bayly						3			
H. searli Sars				1	2	4	2	2	2
CYCLOPOIDA									
Mesocyclops sp.		J	X						
Metacyclops sp. (cf arnaudi)	X			X	X	X	X	X	
OSTRACODA									
Benelongia australis Brady	J							J	
Cypretta baylyi McKenzie		J							
Ilyodromus varrovillius (King)			J						J
CLADOCERA									
Alona sp. nov.						X			
Alonella cf excisa (Fisher)	X	X	X			X			
Amblyorhynchus sp.							X		
Biapertura imitatoria Smirnov					X				
Ilyocryptus sp.					X				
Neothrix armata Gurney	X	X	X	X		X	X	X	X
Rak obtusus Smirnov & Timms						X			
Scapholeberis kingi Sars					X	X		X	X

[1] The form figured by Bayly (1979, figs. 8a-b) not *C. tasmanica subattenuata* (Fairbridge)

Western Australia was at times cut off from two or three islands to the east (Morgan 1980, BMR Palaeogeographic Group 1990) before the seas retreated later in the Cretaceous. Despite the retreat (and the fact that the extensive flooding anteceded Australia's separation from Antarctica), this event may have produced a zoogeographical legacy that has not been obliterated by dispersal. An alternative or additional factor in the distinctness of species assemblages in the southeast and southwest is the marine incursions into central Australia from the Late Eocene through to the mid-Miocene (Nelson 1981).

Pond 3 is the type locality of *Daphnia occidentalis* which was described by Benzie (1986) mainly from material collected during the present study. Benzie (1986) produced evidence that *D. occidentalis* is an ancient relict species whose origins go back at least to the late Cretaceous (*ca* 70 Ma BP). That such an ancient species should presently be known only from highly acidic waters in the present study area may be taken as further evidence that these environments have been in existence in the far south-west of Australia for a long period. The occurrence of an abundance of *D. occidentalis* in pond 3 (pH 4.2-4.5) runs counter to the statement of Okland & Okland (1986) that "the genus *Daphnia* is generally absent below pH 5.0-5.5".

Another ancient relict species that occurs in the region of the Northcliffe ponds, the extraordinary and enigmatic fish *Lepidogalaxias salamandroides* Mees, also has clear acidophilic tendencies; Christensen (1982) showed that the mean pH of waters inhabited by this fish was only 5.4 (range 3.7-6.8). Fifteen specimens of this species were captured in the plankton net at locality 6 on 5 June 1980 when the pH was 3.7.

Calamoecia elongata, which was described by Bayly (1979), occurred in ponds 3, 4, 5 and 6. This species is one of the seven (probably eight) out of the 19 freshwater centropagid species recorded from Western Australia that is endemic to that State (Maly & Bayly 1991, Table 1) and is presently unknown outside the Northcliffe region. The *Paracyclops* Claus occurring at locality 3 is a new species known only from the Northcliffe-Albany region (D W Morton, personal communication) Both of these copepod species are clearly capable of tolerating abnormally high acidity. A peculiar form (new sub-species?) of *C. tasmanica* s.l. (see Bayly 1979 Figs 8a-b) occurred at localities 6 and 7, and is presently known only from acidic waters in that vicinity.

Several acidophilic cladoceran species occurred at localities 3 (Table 5), 4 (Table 6), 6 and 7 (Table 7). *Biapertura imitatoria* Smirnov was described from locality 7 (Smirnov 1989) and is known only from that strongly humic site. *B. longiqua* Smirnov is also acidophilic; Smirnov & Timms (1983) commented that "most of the known habitats are acid waters on sand". *Monope reticulata* (Henry) has not previously been recorded outside of New South Wales where it is "usually found in acid water" (Smirnov & Timms 1983). *Rak obtusus* Smirnov and Timms is known only from acidic waters (mostly in the pH range 4.5-5.5) in New South Wales and Queensland (B V Timms, personal communication) and Northcliffe locality 6 which had a pH of 4.0 on 17 June, 1977 (Table 1).

The very high acidity of some of the ponds did not result in a lowering of species richness. In fact, pond three, whose pH in 1977 and 1980 lay in the range 4.2-4.5 (compared with pH *ca* 6.0 in ponds 1 and 2), yielded 10 species in 1977 and 14 in 1980, and had the highest mean richness within the seven ponds over these two years. This suggests that the micro-crustacean communities of this region (the "southern acid peat flats" of Pusey & Edward 1990) have, over a long period of time, developed an unusually high degree of tolerance of excessive acidity. In contrast, overseas studies (Roff & Kwiatkowski 1977, Confer *et al.* 1983) have reported

a decrease in the species richness of zooplankton communities with increasing acidity. The absence of ostracods from localities 3, 4 and 6 (highly acidic) may be significant. In the Northcliffe region, the age and spatial heterogeneity, for example macrophyte diversity, of a pond, may exert a greater influence on species richness than low pH. The lowest number of species was recorded at localities 4 and 5. Pond 4 was of recent artificial origin and pond 5 entirely lacked macrophytes.

Boeckella geniculata Bayly, *Hemiboeckella andersonae* Bayly and *Calamoecia attenuata* (Fairbridge) are all endemic to south-western Australia but not restricted to acidic waters.

Pusey & Edward (1990) studied two sites (their numbers 8 and 9) located along the Northcliffe-Windy Harbour Road. Their sites were sampled five times over two years, and they recorded 14 taxa of micro-crustaceans. Ten taxa common to their survey and the present study were: *Calamoecia attenuata*, *C. tasmanica* s.l., *Macrocyclops albidus* (Jurine), *Metacyclops* sp. (cf. *arnaudi*), *Cypretta*, *Ilyodromus*, *Biapertura*, *Neothrix armata* Gurney, *Simocephalus* and *Chydorus*.

Bunn & Davies (1990) maintained that the stream fauna of south-western Australia is impoverished, not only in world comparisons, but also relative to that of south-eastern Australia. Regarding the latter comparison, the existing data for the micro-crustaceans of temporary standing waters are rather too limited, not readily comparable, and somewhat contradictory. Morton & Bayly (1977) found some 60 taxa in their study of 53 pools in Victoria whereas the present study found 35 taxa in seven ponds. Lake *et al.* (1989) recorded 30 taxa from a Victorian pond that was sampled 13 times over some seven months, but the Northcliffe pond with the richest assemblage (locality 3) yielded only 15 species from 13 samplings restricted largely to the month of June (but in more than one year). Some evidence contradicts these apparent trends; the total non-marine centropagid fauna (belonging to the genera *Boeckella*, *Hemiboeckella* and *Calamoecia*) of Western Australia amounts to 19 species while that for Victoria and Tasmania is 17 and 15 species respectively (Maly & Bayly 1991). Except possibly for *Calamoecia gibbosa* (Brehm), all of the Western Australian calanoids listed by the latter authors occur in the South West Botanical Province (within Western Australia the great majority of calanoids are found only there) so species density is similar in both regions; the South West Province of Western Australia and Victoria are of very nearly equal area (see Marchant 1973). Perhaps the more common ability of lentic taxa to produce resistant eggs has prevented exceptionally dry periods from extinguishing species to the degree suggested by Bunn & Davies (1990) for the stream fauna of south-western Australia.

Some observations are possible on species succession in this study. The 1977 sampling was instructive from the viewpoint of early succession. Amongst the calanoids, *Hemiboeckella searli* Sars was one of only three species encountered on the first sampling date (3 June) in 1977; at locality 3 (Table 5) none of this species was mature but copepodite stage V had been reached, and at locality 6 (Table 7) the population was very largely immature but a few adults were already present. If it is assumed that localities 3 and 6 came into existence at the break of the wet season, then, with temperatures that prevail in this region, it is inferred that this species is capable of developing from a resting egg to an adult in 19 days. However, allowing for delays in run-off before ponding occurs, the true time for completion of the life-cycle would be shorter than this. The population of *H. searli* was more advanced at locality 7 on 3 June, but this site was at the very bottom of a major depression, the deepest at first sampling (Table 1), and probably the first of the series to contain water. Bayly (1978) pointed out that *H. searli* (and *Hemiboeckella* generally)

shows an exceptionally high degree of sexual dimorphism in size. I suggested that this might enhance the efficiency of food exploitation by allowing the consumption of an exceptionally wide range of particle sizes in situations such as a temporary pool immediately after formation where interspecific competition is likely to be minimal.

Certain other species also appear characteristic of the very early phases of succession, perhaps qualifying as fugitive species *sensu* Hutchinson (1951). Thus *Metacyclops* sp. (cf. *arnaudi*) appeared very early at localities 5-7 (Table 7) in agreement with the findings of Morton & Bayly (1977) and Lake *et al.* (1989) for *M. arnaudi* (Sars) in temporary waters in Victoria.

In 1980, sampling commenced too long after the break of the wet season for observation of early stages in succession. However, two observations, together indicating variable behaviour of *Hemiboeckella andersonae*, are possible. First, at locality 1 (Table 3) juvenile calanoids only were present from 8-17 June to be replaced by mature individuals of *H. andersonae* on 20 June which was 65 days after the break of the wet season. Second, at locality 2 (Table 4) the disappearance of a population of *H. andersonae* was observed; by 17 June it was scarce, on 20 and 23 June a very few adults were found, and by 26 June (70 days after the break) none were found. At this point, *Calamoecia attenuata*, which on 5 June was scarce, was still abundant at locality 2.

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Preliminary evaluation of strontium isotope ratios for dating in the subsurface of the Carnarvon Basin, Western Australia

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Abstract

The results of an experimental programme to evaluate the potential application of Strontium^{87}/Strontium^{86} ratios as a dating method in the subsurface of the Carnarvon Basin are presented and discussed. Age estimates from Sr ratios consistent with independent palaeontological dating were obtained from two samples, one from the Middle Jurassic and one from the Late Jurassic. The samples were from relatively deeply buried sequences (1784 and 2923 metres) indicating that diagenesis need not alter strontium ratios in the deep subsurface. The method shows considerable promise for dating in the subsurface of WA and for correlation within Australian basins and to sections abroad, provided suitable sample material is available. Its usefulness in dating for pre-Tertiary sequences is at present limited and further research is required to refine the pre-Tertiary sea-water $^{87}Sr/^{86}Sr$ curve.

Introduction

The ratio $^{87}Sr/^{86}Sr$ appears to be constant throughout the present oceans and seas of the world. Faure (1986) quotes the present ratio as 0.70906 ± 0.00003 and suggests that the excellent mixing is due to two factors. Strontium has a long residence time of about 5 million years compared to the mixing time of oceans of about 1000 years. Secondly, the concentration of Sr in oceans is high compared with average river water (7.7 micrograms/gram and 0.068 micrograms/gram respectively). The same perfect mixing may be presumed to have occurred throughout Phanerozoic time. However, the ratio is not constant and has varied systematically in the past, reflecting variations in input of strontium to the world's oceans. Animals and plants that build a calcareous skeleton record the strontium ratio of the water in which they exist. By measurement of $^{87}Sr/^{86}Sr$ ratios on carbonate material, Burke *et al.* (1982) estimated the variation of the ratio throughout the Phanerozoic. If their best fit curve for the sample spread is accurate (see discussion below), then determining the ratio in fossil fragments in which strontium has not been added or removed during diagenesis provides a method of dating by comparison with the curve, provided the approximate age of the sequence is known. The ratio does not provide an absolute age by itself, as the same ratio can occur more than once within the Phanerozoic (see below).

The aim of this study was to determine if the ratio could be determined in fossil fragments from palynologically dated subsurface samples and if the resulting ratios were in agreement with the relevant part of the curve as presented by Burke *et al.* (1982). We have obtained $^{87}Sr/^{86}Sr$ ratios on selected carbonate fossil fragments from Jurassic sequences within the Carnarvon Basin of Western Australia, in order to assess the possible wider application of this technique to the hydrocarbon-rich basins of the Northwest Shelf. The Jurassic was selected for the test as it has considerable economic importance as an oil reservoir and source and is relatively deeply buried in the offshore Carnarvon Basin.

Experimental Procedure

Six samples were collected from three petroleum exploration wells in the Carnarvon Basin (Fig 1). The samples were selected from available cores with fossil fragments visible in parts. Treatment of three of these samples in the laboratory with dilute hydrochloric acid indicated that the fossil fragments were partially or completely dolomitised; these were not analysed further because of the risk that the strontium content was different from the original. Three samples contained fragments of belemnite guard which were still composed of calcite. The strontium content of these fossil fragments was determined by atomic absorption analysis and was found to vary from 5387 to 5096 ppm (Table 1). Veiser (1983) reports that belemnites average about 4000 ppm Sr; these samples were thus judged to retain more or less their original strontium content.

Table 1

$^{87}Sr/^{86}Sr$ Ratios obtained by analysis. Letters a, b and c refer to repeat analyses performed on material from the same sample. Values are means ± standard deviation. The error was considered too great to provide a reliable $^{87}Sr/^{86}Sr$ ratio for the sample from Bambra-1.

Sample (depth,m)	Sr Concentration (ppm)	$^{87}Sr/^{86}Sr$
NBS 987 (standard)		a: 0.710235 ± 0.000007
		b: 0.710238 ± 0.000028
		c: 0.710231 ± 0.000014
		mean: 0.710235
Rosemary-1 (2923m)	5387	a: 0.707039 ± 0.000014
		b: 0.707065 ± 0.000007
		mean: 0.707052
Anchor-1 (1784m)	5344	a: 0.706941 ± 0.000014
		b: 0.707067 ± 0.000014
		mean: 0.707004
Bambra-1 (2726m)	5096	a: 0.707470 ± 0.00345
		b: 0.707038 ± 0.00026
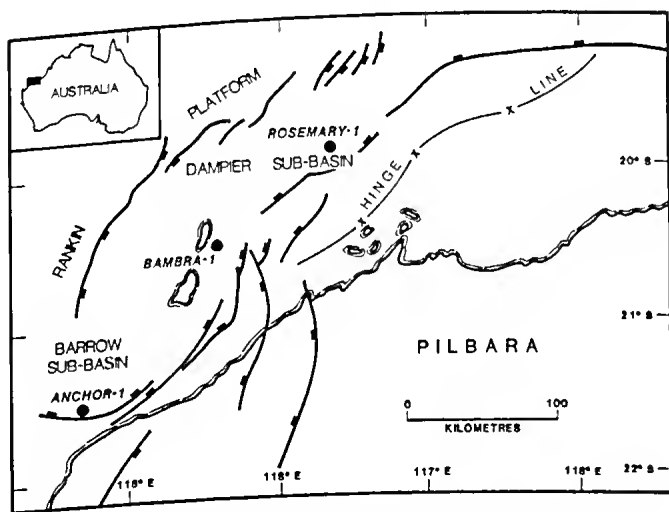
Figure 1 Northwest Shelf of Western Australia: Location of wells from which samples were analysed.

Further samples of the belemnites were coarsely crushed and small fragments with fresh surfaces were hand-picked. Approximately 100 mg of these chips were dissolved overnight in a teflon beaker in 1 ml of 6N HCl. The solution was then evaporated on a hot-plate in a class-100 clean air environment. This procedure was repeated until all the carbonate was dissolved. The solution was then re-evaporated, redissolved in 1N HCl and loaded onto a preconditioned column of Dowex-50 cation exchange resin. After washing with a measured volume of 2N HCl, Sr was isolated in 6N HCl. The solution was then evaporated and approximately 50-100 micrograms of Sr was loaded onto a single Re filament assembly. Sr was analysed on the VG-354 multi-collector mass spectrometer at Curtin University. Recent experience indicates that the best results are obtained using a peak-jumping procedure and a single collector. Multiple analyses of the NBS-987 Sr standard indicate an external precision of ± 0.000016 (1 standard deviation, n =12).

Results

Results including analysis of the NBS 987 standard, are presented in Table 1.

The sample from Rosemary-1 (2923m sub-KB) is within an interval dated by palaeontology in the well completion report (Anon 1973) as Callovian to late Bathonian. The Sr ratio from this sample of 0.70705 plots on the 'Burke Curve' (Burke et al. 1982) at approximately 170 million years (Fig 2). The Callovian to Bathonian on Van Eysinga's (1975) time scale, used by Burke et al. (1982) is between 160 and 167 million years.

The sample from Anchor-1 (1784 metres sub-KB), dated palynologically in the well completion report (Andrejewskis 1969) as Tithonian gave a ratio of 0.70700, which plots on the curve at about 145 million years. The Tithonian on Van Eysinga's scale is between 141 and 145 million years.

The results from Anchor-1 and Rosemary-1 are thus in good agreement with the palaeontological data.

The sample from Bambra-1 (2725.7m sub-KB) did not produce values within an acceptable error.

Discussion

These results indicate that the Sr ratio method has considerable promise as a dating and correlation tool in the subsurface of Western Australia. There was close agreement between dating by fossils and by Sr ratios in two out of the three samples studied. However, the results can only be considered a preliminary test. The method can provide an absolute value or series of values, provided suitable sample material is available. The method only requires small quantities of well-preserved carbonate material which can be in the form of fossil fragments. This is a considerable advantage in subsurface analysis. However, as an dating technique, there are still considerable limitations to its use. The approximate age of the sample must be known. The ratio 0.7070 for example occurs four times in the Jurassic and Permian on the 'best fit' Burke curve (Fig 2). The 'best fit curve' has been determined from a
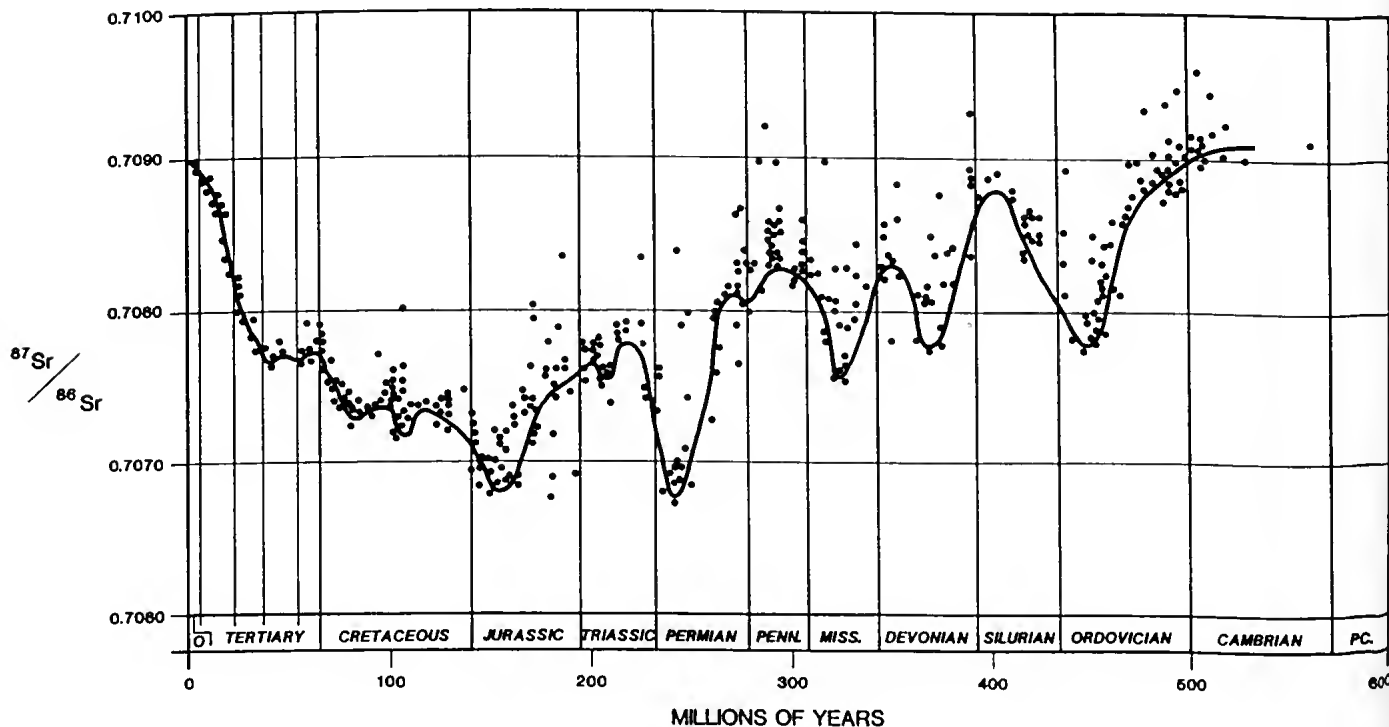
Figure 2 The 'Burke Curve' of the variation of $^{87}Sr/^{86}Sr$ ratios with time in the world ocean, based on the analysis of 744 samples. The line represents the best-fit curve through the data; modified from Burke et al. (1982).

wide spread of results in the pre-Tertiary. The spread increases with increasing age. Burke *et al.* (1982) suggest four possible reasons for this:

1. The strontium ratios of the samples are in some cases not representative of the world ocean.

2. Small but relatively rapid fluctuations may have occurred at times in the past, and thus the curve may be more variable than shown.

3. Errors may have occurred in the palaeontological dating of samples analysed for constructing the curve.

4. Diagenesis has altered the Sr ratios in the samples since deposition.

The extent of the potential problem with diagenesis can be minimised by analysing samples composed of low-magnesian calcite, diagenetically the most stable form of $CaCO_3$. Belemnite fragments are thus suitable and possess the added potential advantage that they were an open-ocean nektonic faunal element, and may be expected to have retained an open ocean strontium signature, minimising potential problems with nearshore variations in strontium ratio. Excluding samples that appear to contain an altered strontium content should also improve the accuracy. Burke *et al.* (1982) found they were able to define a better curve by ignoring samples with a Sr content lower than 200 ppm, and samples with a high insoluble residue.

The problem that samples may not be representative of the world ocean signature may be particularly acute at times of warm global climate. Today, the world ocean is well mixed, reflecting the vigorous circulation driven by the cold polar areas. At times of widespread oceanic anoxia, in the Mesozoic, the ocean was possibly not well mixed and a variation in strontium ratios, particularly in isolated embayments or broad shallow seas could have occurred. It is interesting to note that the widest spread of samples from the best fit curve in the Cretaceous occurs at around 100 million years, coincident with the maximum development of the Aptian-Albian oceanic anoxic event (itself the best developed and longest lasting oceanic anoxic event recognised in the Cretaceous (Jenkyns 1986).

A fundamental problem with the 'Burke curve' is raised by the question of accuracy of palaeontological dating of samples which form the basis of the curve. At present, the magnitude of the error cannot be determined because *where* the error occurs is unknown—is the age wrong or is the strontium ratio wrong or are they both wrong? The curve will only become really useful if accurate ratios can be determined for individual stages at their type sections where the ages of zones and substages are known by definition. A Phanerozoic curve could then be constructed from the determination of individual type sections. Such determinations will also show if there have been short term fluctuations in the $^{87}Sr/^{86}Sr$ curve which are not apparent in the general curve.

Finally, the curve may be improved by careful sampling of single faunal elements, preferably of low magnesium calcite rather than bulk carbonate samples. It is not clear if Burke *et al.* (1982) used bulk rock samples or individual faunal elements, but other studies, such as Faure *et al.* (1978) and Tremba *et al.* (1975) were based on analysis of bulk samples and their results are not particularly consistent with the 'Burke Curve'. Complex diagenesis in carbonates is the norm, and it is easy to envisage different elements that make up the rock attaining different strontium contents during diagenesis. Consistent, repeatable results would not always be expected therefore from bulk sample analysis.

The strontium ratio method of dating and correlation shows considerable promise for use in subsurface studies, provided material which retains the original signature of the Sr ratio is available for analysis. There are a number of problems to be overcome before the world curve is accurate or unambiguous enough for widespread use. Determinations of the variation of the ratios in stage type sections needs to be undertaken. The method will never replace dating by other means, particularly palaeontological dating, because very few $^{87}Sr/^{86}Sr$ ratios are unique to one time. The ratio 0.7080, for example, occurs 7 times in the Palaeozoic and once in the Tertiary. The method is also of no or limited use around points of rapid change from an increasing to a decreasing ratio. Although the method is only really useful in the Tertiary, where control is good and the curve well and unambiguously defined, it will find wider application in older sequences as the sea-water Sr isotopic variation curve becomes better defined. The method is relatively quick and requires very little sample material. It can be performed on fossil fragments and has particular application in stratigraphic correlation between boreholes.

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Atmospheric Turbidity Measurements at Broome
in
Western Australia 1979-1984

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Abstract

A special version of a Voltz, hand-held sun photometer was used to measure direct solar radiation several times each day at the meteorological station at Broome aerodrome from 1979 to 1984. These data were fully compensated and corrected and interpreted in terms of atmospheric turbidity using precise solar calculations. Calibration included extrapolation to zero air mass (Langley plots) and cross-comparisons. The data show no synoptic or mesoscale variation but a seasonal variation with higher values near the end of the dry periods. Calculated wavelengths exponents show smaller particles are present in these dry periods. A harmonic analysis shows that 20-25% of the variance is explained by an annual cycle, 10-15% by a cycle of 3 years, and that turbidity increases 7-11% per year. Bushfires and marine aerosols are likely to be important contributions to the trends though effects of the volcanic eruption of Galunggung are apparent in 1982-1983.

Introduction

The occurrence of dust storms from the Australian continent and the movement of volcanic dust clouds through the area is important on a global scale. It is known that dust storms over Australia inject large quantities of mineral aerosols into the atmosphere during the September-October and February-March periods (Middleton 1984). Dust clouds have been known to spread out in a plume that covers a large portion of the Indian Ocean (Bell 1991, McTainsh *et al.* 1989). The importance of this quantity of aerosol to the radiation budget of the area and the global energy budget should not be underestimated (Kondratyev 1972).

Burning is another concern; it raises elemental carbon and, through subsequent photochemistry, ozone levels. A spring maximum from biomass burning may be propagated throughout the southern hemisphere (Heintzenberg & Bigg 1990). A seasonal cycle in ozone is observed over Indonesia with a maximum in the March-April period when biomass burning is most common (Fishman *et al.* 1990). The Kimberley area of Western Australia is frequently heavily burnt; the area burnt by each individual fire increases with time after cessation of the rainy season (Bell 1981, Haynes 1985). In late 1984 a bushfire plume was evident over Broome (J L Gras personal communication).

In addition, during the period 1979-1984 a number of eruptions of volcanos affected the turbidity (τ) or Aerosol Optical Depth (AOD; considered identical to turbidity in this paper) in the southern hemisphere. The major eruption of El Chichon in Central America in April 1982 has been shown to have affected stations in the Antarctic (Etheridge 1984). Several Indonesian volcanos were also active in 1982 (Scientific Event Alert Network 1981, 1982). The stratospheric aerosol level increased from late 1982 through to 1984 from these volcanic eruptions (Gras *et al.* 1986). In particular, eruptions of the volcano Galunggung in Indonesia produced ash clouds that were shown to have passed directly over Broome in July 1982. A study of the passage of the Galunggung and El Chichon plumes over Broome and the relative values of τ during their passage should help quantify the way volcanic aerosols move and disperse. Such aerosols not only decrease the intensity of solar radiation but also damage high flying aircraft (Creagh 1992).

With the conception of the Global Weather Experiment a number of aerosol monitoring stations were established around the globe. Along with other instruments these stations contained sun photometers modelled after the design of Voltz (1959). One such station at Broome in the northwest of Western Australia measured the intensity of direct solar radiation from May 1979 to November 1984. This data set is one of the longest consistent measures of turbidity in the southern hemisphere. This paper describes the calibration procedures used on the instruments and reports the calculated values of τ (AOD) and the wavelength exponents. The results are interpreted in terms of known volcanic activity and cyclic trends in the troposphere and stratosphere.

Materials and Methods

Location and Meteorology

Broome is located at 17° 57′ S latitude and 122° 15′ E longitude and generally experiences the wet and dry periods of the tropics in southern latitudes. During the wet half of the year (December to April) the surface low pressure area over the inland tropics produces low level west to southwest winds over the Broome area. The surface wind flow is characterised by a generally light to moderate flow that is strengthened near the coast by a sea breeze. At atmospheric pressure levels between 850 to 500 mb winds are predominantly easterly. Tropical depressions and cyclones occasionally affect the area in this period and often result in strong easterly winds at all levels below 500 mb. In the dry half of the year the middle latitude ridge moves northwards and consequently easterly winds prevail below 850 mb while westerlies dominate above this level.

The Sun Photometer

The instruments used in the study are improved versions of the instrument of Voltz (1959). Instrument specifications are listed in Table 1. Note that the photometers are hand-held and a scanning procedure is used to detect the direct radiation coming from the sun. A peak sample-and-hold circuit is used to store the maximum measured signal from the silicon photosensor. The sensors are affected by temperature with approximately 0.1% change in response per degree Celsius. The temperature drift of each sensor is given by the manufacturer and was remeasured at the University of Miami (by Tom Snowdon) and a linear regression line fitted to data. In-field compensation was achieved by a thermistor thermometer built into the units. A FORTRAN program interpreted the maximum voltage measurement after compensating for temperature, and calculated the precise solar position and the final value of τ. Various versions of this program were generated by David Pascoe, William Scott and Bruce Forgan (see Acknowledgements and Herman *et al.* 1981).

Table 1

Specifications of the University of Miami
Series 300 Sun Photometer

Interference Filters:
    (Located in filter wheel)
    Red*—875 nm with 16 nm half width
    Green—500 nm with 10 nm half width
    Blue—380 nm with 11 nm half width.
    manufactured by Microcoatings, Inc.
    * bonded to a disk of UG1 Schott glass 1 mm thick for Infrared cut-off.

Detector:
    (Located 8 cm behind the filter wheel)
    Bell & Howell type 529-2-5
    Silicon Photodiode of 5 mm area.

Optics:
    Approximately a 2° viewing angle in UM 321. Photometer UM 318 has a viewing angle of 1°, achieved by adding a 271 mm tube with a front aperture 7.14 mm in diameter.

Two different instruments were used in the study: UM321 from May 1979 to July 1981, and UM318 from July 1981 to November 1984. Photometer 318 was identical to 321 except that it was fitted with an additional optical tube to provide a viewing angle of 1 degree. This tube improved the sensitivity and stability of the optical depth measurements. Both instruments measured the intensity of direct solar radiation at four wavelengths: Blue (380 nm), Green (500 nm), Red (880 nm), and Water (945 nm); the near infrared Water (945 nm) measurements are not reported here. Filter characteristics are listed in Table 1.

Measurements were taken when possible in the early morning, midday and late afternoon. This allows for partial *in situ* calibration should there be a temporal change in the instrument electronics or optics (J M Prospero, 1978: Manual for Series 300 RSAMS Sun Photometers, unpublished).

Calibration

The two instruments were calibrated in 3 ways:

1. Langley plots before and after the experiments and during comparison experiments

2. Daily *in situ* calibration

3. Cross-calibration with one another and standards.

The Langley analysis assumes a constant optical depth during the measuring period (usually one day); plotting the output voltage as a function of known air mass allows the values of the voltage that would be measured at zero air mass (J_0) to be obtained by extrapolation. At the chosen wavelength this voltage corresponds to the sun's intensity outside the atmosphere at a mean sun-earth distance (Kondratyev 1972).

Langley plots of the instruments' response were completed on several occasions including pre-use and post-use. Fig 1 shows the extrapolation for 11 February 1981, 13 February 1981 and 13 April 1983 for photometer UM321. Note that data from 14 February 1981 overlayed the data of 11 February 1981 and are not shown. The resulting calibration J_0 constants are listed in Table 2. These measurements are made at different wavelengths; they must be made on relatively clear days with a consistent τ. In addition, especially at low sun elevation, the time between measurements should be less than 1 minute. The statistics of the calibration should follow Herman *et al.* (1981). Practically it is found that refractions and local effects become important above air mass 2.5; it is preferable to have at least 5 measurements at equally spaced intervals between air mass 1 and 2.5.
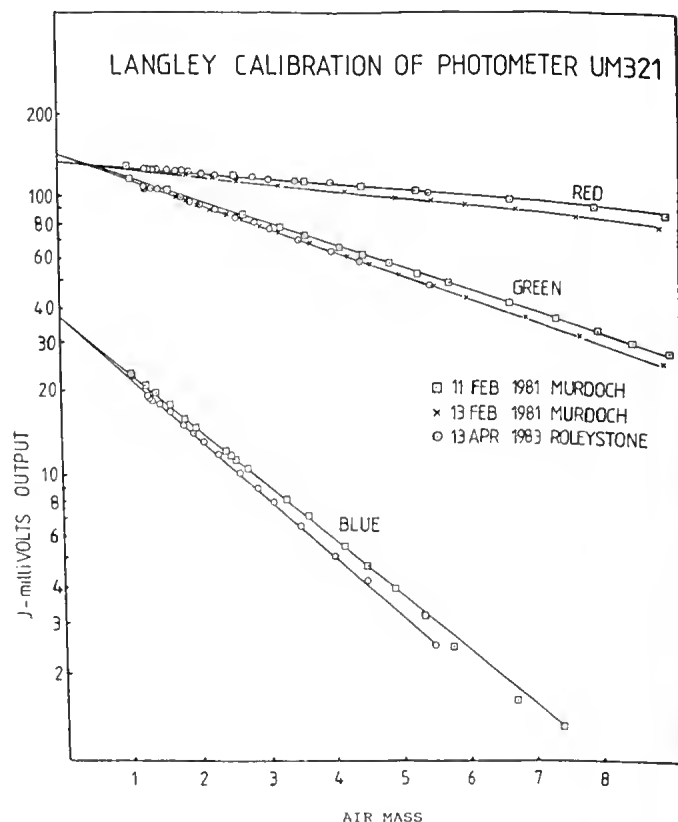
Figure 1 Extrapolation of the measured output of photometer UM321 to zero air mass. This Langley analysis produces the calibration J_0 values (see Voltz 1978).

Calibration data were also obtained by using daily *in situ* data collected at Broome. With typically six data cycles per day, the Langley method was used on the limited morning and afternoon data cycles, hereafter called the short Langley technique. Data were edited to remove those days in which the morning and afternoon total optical depths, derived from the short Langley analysis, were markedly different, or less than the assumed molecular optical depth (see end of section for an explanation). *In situ* calibrations

Table 2

Results of Langley Calibrations for J_o

Instrument	Filter	Original Calibration[1]	February 1981	13 April 1983	Form used for data—Based on *in situ* calibration
	Blue (380 nm)	41.2 mv	38	37	38.2
UM321	Green (500 nm)	159.5 mv	143	140	151.1 − 4 (T-1979)
	Red (880 nm)	135.3 mv	134	134	133.2
			11 May 1981	22 December 1984	
	Blue (380 nm)		58.4	42	55.13 − 1.866 (T-1981)
UM318	Green (500 nm)		201.6	199	202.4 + 1.484 (T-1981)
	Red (880 nm)		174.6	165	169.4 − 0.6 (T-1981)

[1] University of Miami (1978).

were then performed on all data for the remaining days (air masses below 6.0). The resulting extrapolations were then averaged for the month. These produced consistent trends in the calibrations at several wavelengths. These trends were statistically significant and were used in the processing of the data.
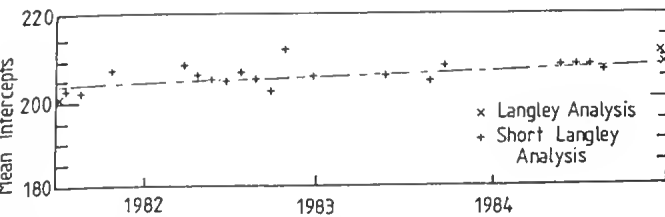
Figure 2 Comparison of the *in situ* values for J_o from the short Langley analyses with the values for pre- and post-Langley analysis.

The *in situ* results compared well with the Langley analyses prior to and after collection of the data set. A plot of the results of the short Langley analysis for UM#318 at 500 nm is shown in Fig 2, together with the values derived from special Langley calibration analyses mentioned above. The upward trend evident in the figure proved to be a function of the gradual rotation of the sensor by mechanical vibration over an extended period. When returned to its original position, the 500 nm calibration returned to within 1 per cent of the original 1981 Langley calibration.

Cross calibrations were completed when the instruments were traded and at the end of the sampling period. These amounted to making nearly simultaneous measurements. As expected, the correlations between like wavelengths were high in each series and confirmed the drift shown by the other calibration methods. The correlation coefficients between photometers UM318 and UM321 on 10 June 1981 ranged between 0.95 and 0.98; on 22 December 1984 between 0.93 and 0.97.

Additional comparisons with state-of-the-art World Meteorological Organisation (WMO) design sun photometers, at the Cape Grim Baseline Air Pollution Station in Tasmania, also confirmed the end calibration values, after small corrections were made for the difference in central wavelengths.

Processing the Data

A precise algorithm (developed by B Forgan and D Pascoe), was used to obtain the zenith angle of the sun θ and the mean earth-sun distance. Then the air mass, m = secant θ, was used to obtain the optical depth at the mean earth-sun distance at m = 1.0:

$$\tau = \frac{\ln J/J_o}{m} \qquad (1)$$

where J is the measured signal and J_o the calibration constant related to the true earth-sun distance. Corrections were made for ozone absorption and molecular scattering affects by subtraction.

The molecular optical depth was determined from the functional form given by Frohlich and Shaw (1980) but with corrections determined by Young (1981). Ozone coefficients were those recommended by the World Meteorological Organisation (1982).

During the period of very low τ, a small number of the derived values were either zero or negative. These data were ignored in the analysis presented below. Quality control analyses suggest that the negative values occurred through unaccountable instrument drift or transcription error (see Discussion). For a single observation at unit airmass, error analysis suggests a precision of 0.010 in the results for τ_{500}, 0.020 for τ_{380} and 0.006 for τ_{875}.

The data were later interpreted using a harmonic analysis and a separate frequency analysis. Bloomfield (1976) presents the procedures for both techniques. The analyses were completed using a Vax 780 computer at the University of Miami using library routines for the required FFT (Fast Fourier Transform) analysis and matrix inversions. The harmonic analysis fits the data to a set of frequencies that are multiples of the lowest frequency (about 5.5 year) using as many harmonics as are required to sensibly fit the data. It is a standard technique but suffers from the compounding of errors when solving for a large number of harmonics and doesn't allow for frequencies other than multiples. The frequency analysis is a trial and error method that picks the most significant frequencies independent of whether they are multiples or not. In both types of analysis, the fit gives a minimum of the sum of the squares of the deviations, a 'maximum likelihood' estimation. The frequency analysis is tedious but minimises the calculation error and can easily allow for non-cyclic trends in the data (linear and exponential).

Results

All the data are plotted in Fig 3 as single points relative to the time of day. Note that there is little, if any, preference for higher τ in any part of the day although most measurements were made slightly after solar noon. Several averages were calculated to separate the trends in these data. Fig 4 shows average daily values for the whole measurement period. Other average values are presented in Figs 5, 6, 7 and 8. The lines in Figs 6, 7 and 8 simply connect average values.
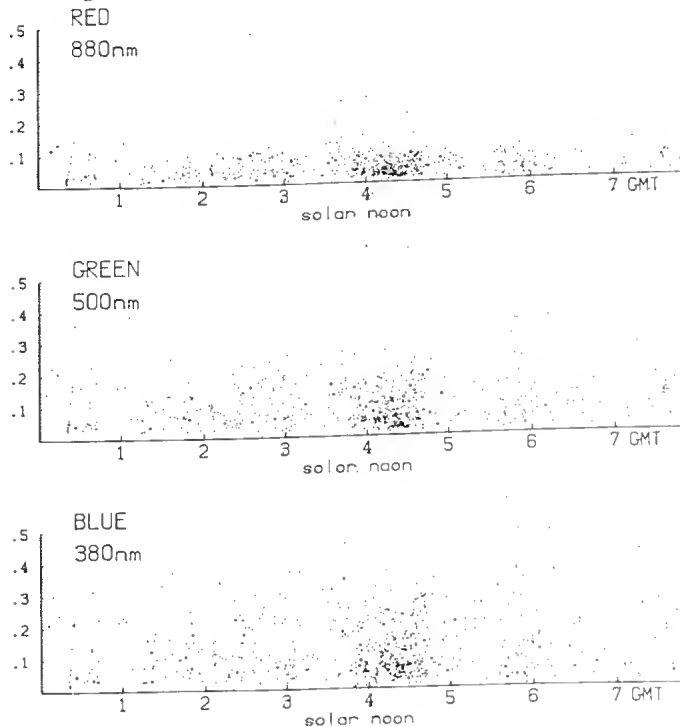
Figure 3 Atmospheric turbidity (τ) values measured at the Broome Aerodrome. All values measured between 1979 and 1984 are plotted as a function of the time of the day.

Generally, few data points were collected in the months of December, January and February because of the high cloudiness. The March and April data dominate. Lowest values occur from April through July; highest, September through November. The values for September through November are typically 2.3 times the values observed from April through July, for all wavelengths. For example, τ_{500} ranges typically from 0.05 in winter to 0.125 in spring.

The seasonal trends of Fig 4 are clear in the overlay of data in Fig 5. Note that these points are weekly averages and the same symbol, rotated, is used for all years. Little, if any of the variation is removed by this averaging; even the monthly averaged values of Fig 6 exhibit most of the variation. Only with yearly averaging (Fig 7) does the variation diminish significantly.

Wavelength exponents:

$$\alpha_{BR} = \frac{-\ln\,(\tau_{Blue}/\tau_{Red})}{\ln\,(380/880)} \qquad (2)$$

$$\alpha_{GR} = \frac{-\ln\,(\tau_{Green}/\tau_{Red})}{\ln\,(500/880)} \qquad (3)$$

give some information on the size distribution of the aerosol particles. They were calculated for each measurement and averaged over various periods. Fig 8 shows monthly averages of these quantities on the lower two
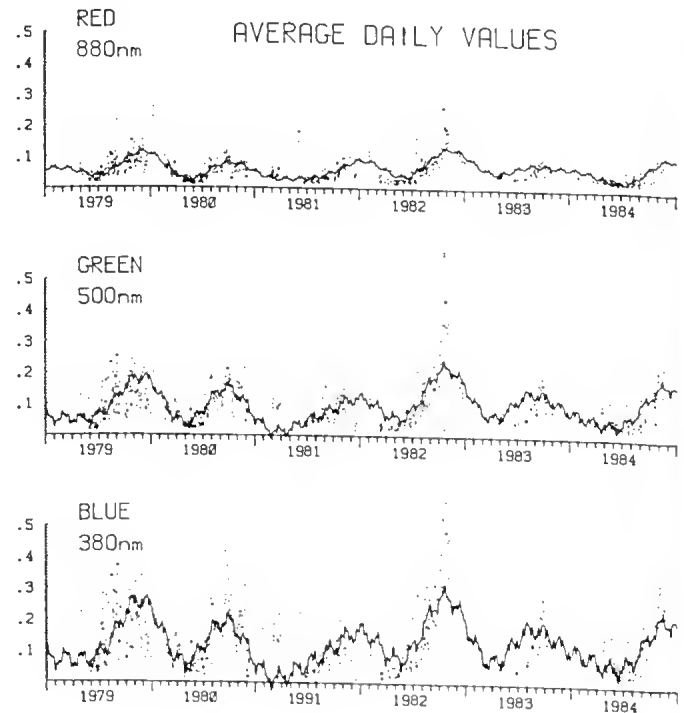
Figure 4 Average daily values of τ measured between 1979 and 1984 at Broome, Western Australia. Fitted curves from the frequency analyses are included (see Table 3).
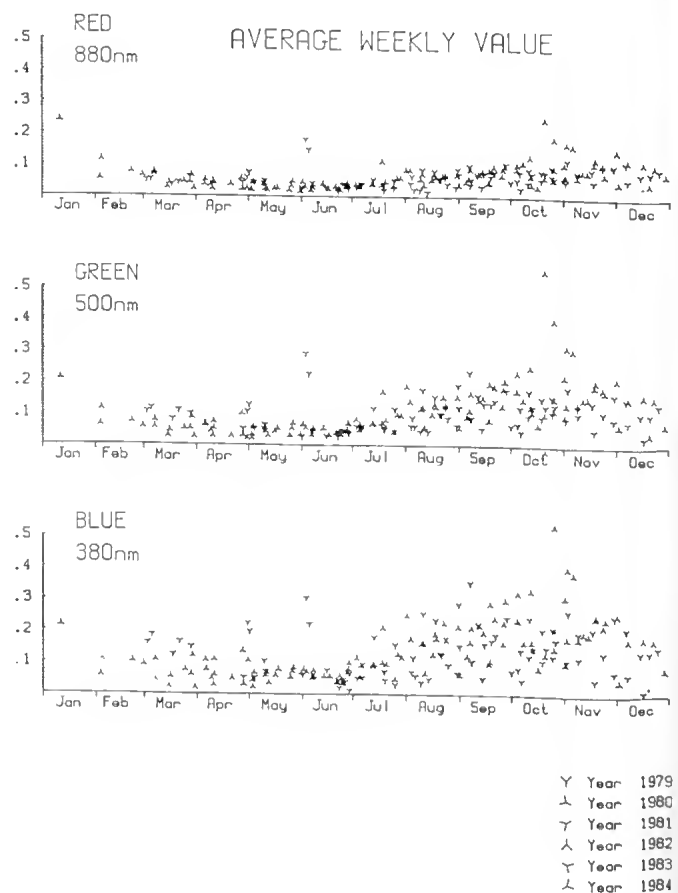
Figure 5 Average weekly values of τ measured between 1979 and 1984 at Broome, Western Australia.

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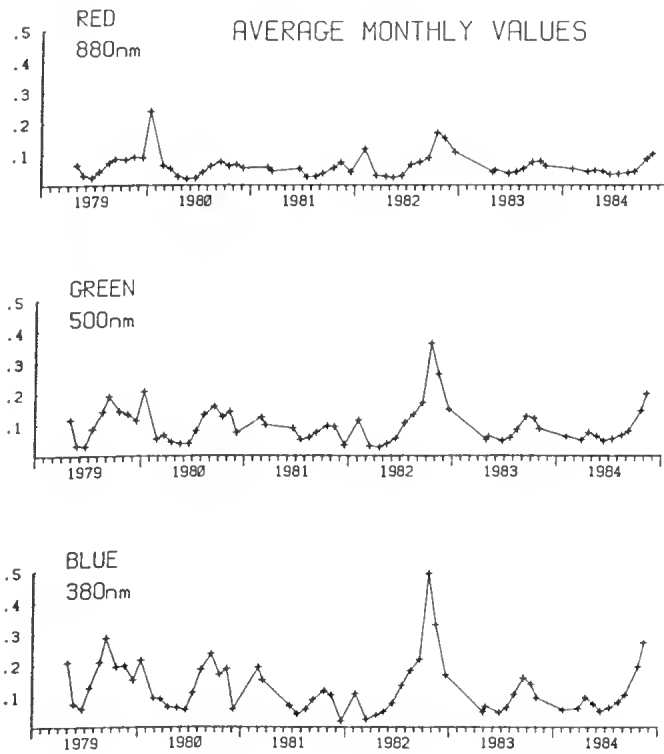
Figure 6 Average monthly values of τ measured between 1979 and 1984 at Broome, Western Australia. Lines join the average monthly values.
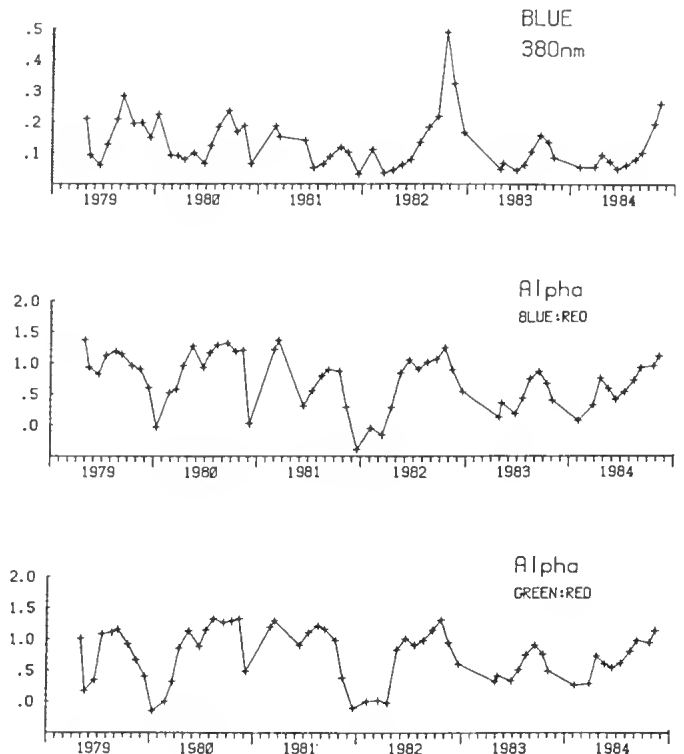
Figure 8 Monthly averaged values for wavelength exponents (α) measured between 1979 and 1984 at Broome, Western Australia are presented on the lower two curves; the τ measured with the blue filter is displayed on the upper curve for comparison.
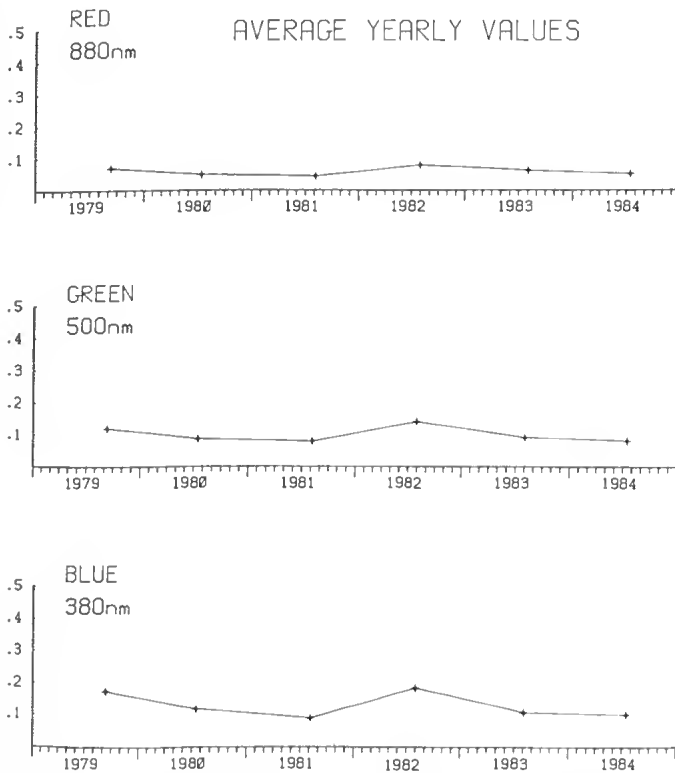
Figure 7 Average yearly values of τ measured between 1979 and 1984 at Broome, Western Australia. Lines join the average yearly values.

curves. A plot was also made of the Blue : Green wavelength exponent; the green values exhibit some anomalies and the combination Blue : Green produced some large negative values of α. Also τ values less than 0.02 were excluded because of the large influence of small (nearly zero) values on the ratios.

The derived α means were lower during April through June for all wavelength pairs. Larger values (greater than unity) occur during September through November. The uncertainties of the α values depend on the season and wavelength pair. A value of 0.25 is a conservative estimate of the error in monthly mean α for all wavelength pairs. The differences between monthly mean α from March-June and August-November periods are 0.3 for α_{BR} and 0.4 for α_{GR}.

The cyclic or nearly cyclic variations in the τ data suggest that a harmonic analysis or a frequency analysis might be appropriate. The harmonic analysis included as many as 50 harmonics and explained as much as 70% of the variance in the data. The effectiveness of the analysis for the Blue optical depth data is represented in Fig 9. Here the number of harmonics is plotted on the abscissa; these are harmonics relative to the entire data set with a period of 5.5549 years or 0.18 cycles/year. The entire data set of approximately 2900 data points yields 643 separate daily average values. The Coefficient of Determination (COD; r^2) is plotted on the ordinate. Note that, in fact, substantial improvements in COD only occur when frequencies of periods 2-3 years, ≅1 year, and ≅0.5 years are fitted to the data; most of the variance in the data is explained by these harmonics. Hence a further frequency analysis was completed following the

method of Bloomfield (1976). This considers selected frequencies that affect the standard deviation and includes a constant and a linear trend. Table 3 is a summary of the results when seven frequencies are allowed;

$$X(t) = \mu + nt + \sum_{j=1}^{7} (A_j \cos \omega_j t + B_j \sin \omega_j t) \qquad (4)$$

The analysis uses a trial-an-error fitting procedure to minimise the sum of the differences (maximum likelihood). here, μ is the mean and n is the linear trend. Seven frequencies were sufficient to fit the data. An annual cycle explains 20-25% of the variance (Table 3).

Table 3

Results of the frequency analysis for atmospheric turbidity in Broome, 1979-1984

	Period	Coefficient	Phase[1]	% Variance explained
Blue (380 nm) (average = 0.1370, sd = 0.1088)				
Mean (μ)[2]		0.1036		
Linear Trend/yr (n/μ)[2]		+0.0075		
		(+7.2%/yr)		
1st frequency	1 year	0.06551	-152°	20%
2nd frequency	2.91 years	0.05124	-61°	11%
3rd frequency	0.716 yrs	0.03471	68°	5%
4th frequency	1.89 mo.	0.02303	2°	2%
5th frequency	4.3 days	0.01314	-10°	0.7%
6th frequency	7.5 days	0.01221	89°	0.6%
7th frequency	5.8 days	0.01144	-45°	0.6%
COD = 0.45				
Green (500 nm) (average = 0.1028, sd = 0.07605)				
Mean (μ)[2]		0.0732		
Linear Trend/yr (n/μ)[2]		+0.0080		
		(+11%/yr)		
1st frequency	1 year	0.05112	-155°	25%
2nd frequency	2.91 yrs	0.03483	-62°	11%
3rd frequency	0.714 yrs	0.02516	57°	5%
4th frequency	1.89 mo.	0.01341	7°	2%
5th frequency	5.8 days	0.00784	-43°	0.5%
6th frequency	7.5 days	0.00737	86°	0.5%
7th frequency	4.4 days	0.00724	16°	0.5%
COD = 0.48				
Red (880 nm) (average = 0.05933, sd = 0.03853)				
Mean (μ)[2]		0.04655		
Linear Trend/yr (n/μ)[2]		+0.0051		
		(+11%/yr)		
1st frequency	1 year	0.02677	177°	26%
2nd frequency	3.05 yrs	0.02045	-38°	15%
3rd frequency	0.715 yrs	0.01526	58°	6%
4th frequency	1.66 mo.	0.00598	-57°	1%
5th frequency	4.38 days	0.00383	103°	0.5%
6th frequency	7.52 days	0.00308	44°	0.3%
7th frequency	6.55 days	0.00303	-46°	0.3%
COD = 0.56				

[1] The phase is relative to the start of 1979. Note that the phase and significant digits are retained to calculate the cyclical waveform in Figures 4 and 10.

[2] see equation 4.

Of course, it is not possible to resolve whether the trend is part of a longer term variation. The three-year trend itself is of doubtful validity in only a five-year time series.

The higher frequencies are only included for interest; they appeared in the objective analysis but are unlikely to be significant. Several simulated data sets with known periodicities and the same temporal sequence were subjected to the same analysis; the result was an error of about 5% in the coefficient and 10% in the variance.
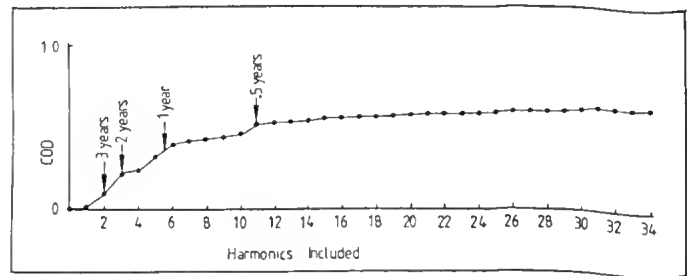
Figure 9 The Coefficient of Determination (COD; r^2) produced by the inclusion of various harmonics in the harmonic analysis of blue optical depth data.

The results of the frequency analysis were used to produce the curves shown in Fig 4 and Fig 10. These curves are produced by recombining the cyclic terms and the linear terms to produce a cyclic curve. Using the data in Table 3, the entire data set can be reproduced as the line presented in the graph. The most significant variations are shown by using the three most significant frequencies and the linear trend, as shown in Fig 10. The more oscillatory line in Fig 4 is produced by using all seven frequencies; the daily averaged data are also shown. The fit is acceptable but there is no justification for incorporating the high frequency variations.
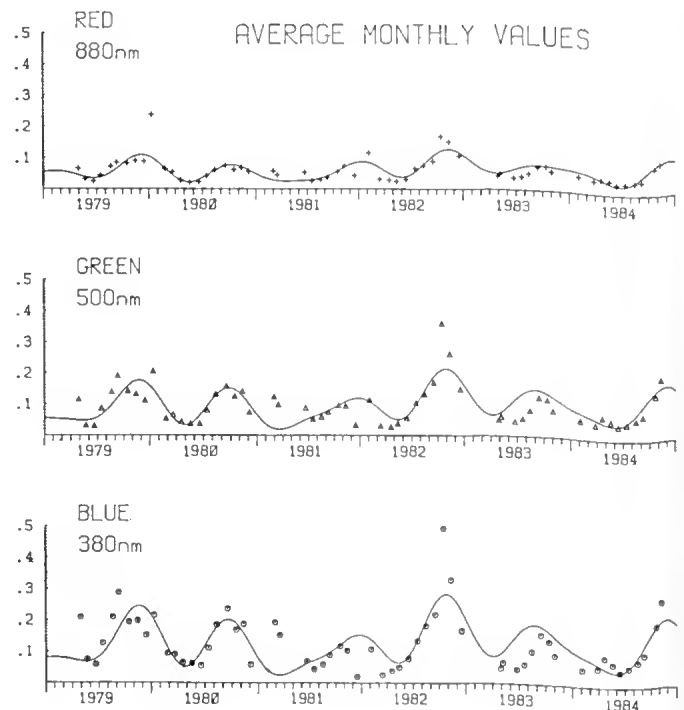
Figure 10 Fit of the data with a frequency analysis using only the three most significant frequencies (see Table 3). Data points are monthly averaged values of τ (see Fig 6).

Discussion

The seasonal nature of the atmospheric turbidity data is clear from Fig 10 where the points represent monthly averages. The variation from one year to another is marked, especially in the onset and duration of the maximum in the dry period.

The aerosol optical depths are influenced by at least two temporally dependent processes. Seasonal changes in the winds with aeolian generation of aerosol and bushfires or man's activities, and longer term trends due to stratospheric containment. The first influence is likely to be cyclic; the latter, single near random injections that gradually die through slow exchange with the troposphere. It is clear that local mesoscale trends or synoptic trends are insignificant in the data. Specifically, the objective fitting procedures (see Table 3) reveal that less than 2% of the variance can be explained by such trends. The annual cycle is easily accepted but the three year cycle is not. Though this longer cyclic effect may even be derived from some northern hemispheric influence, it is most likely a result of two or more volcanic eruptions in 1979 and 1982. Pulse injections effectively contain every possible wavelength and with time and dispersion the longer harmonics are all that remain.

The annual cycles of aerosol optical depth and wavelength exponent suggest a predominance of smaller particles in the aerosol during dry periods with a maximum in aerosol optical depths at all wavelengths. This has been observed by Angstrom (1970) in broad-band turbidity studies of northern hemisphere stations. Similar trends were also observed by Forgan (1977) in continental Australia. In the wet periods, about the end of each year, minimum values of α occur (see Fig 8). The maxima in α may result from the greater infusion of continental aerosol and the increased bio-activity and burning of the dry period. The minima in turbidity and wavelength exponent with the onset of the wet period is influence by removal or aggregation of smaller particles by moist processes.

Contributing also is the marine air mass that passes over Broome in the wet season (see Fig 4), December to April, when surface winds are from the Indian Ocean, and large salt particles predominate in the clean, maritime air. Later, in the dry season, burning-off effects are likely to contribute an ever-increasing amount of aerosol. There is an increase in turbidity and an increase in α, just before December. The dramatic pulse in turbidity observed in the September-November period of 1982 shows no apparent influence on the wavelength exponent. Though this pulse is likely stratospheric and volcanic, it is similar in overall size to the continental aerosol.

The data from 1982 and 1983 (see Fig 6) were affected by the injection of volcanic aerosol that derived from a series of eruptions from volcanos Galunggung (Indonesia) and El Chichon (Mexico). The 1983 effects are carried over from eruptions in late 1982. Satellite evidence of the influence of Galunggung volcanic plumes in the stratosphere on the radiation budget of western Australia has been reported by Bell (1983). The influence of El Chichon on global radiative transfer has been examined in numerous studies (see Bandeen and Fraser 1982). The data presented by Spinhirne (1984) for southern latitudes in October 1982, suggested that the effect of the El Chichon had reached 35°S. Evidence obtained from the Broome record suggests initial increases in τ from July to September 1982 at 20°S could be related to the large eruptions from Galunggung and that the dramatic influence of El Chichon was only evident in late October (Scientific Event Alert Network 1982). The temporal extent of the increase in aerosol optical depth can also be attributed to the simultaneous passage of the El Chichon cloud band south of 20°S. Aerosol optical depth data for 500 nm reported by Francey and Forgan (1986) for Cape Grim in Tasmania at 41°S, also shows an initial increase over the background level of between 0.05 and 0.07 to September, 1982. At Broome the major increase occurred in late October, while at Cape Grim the major increase attributed to El Chichon occurred in February 1983. The magnitude of the increase in τ at Cape Grim is of a similar magnitude to the November data at Broome.

It is important to recognize the limitations of the data set. Errors in the data are around 0.01 in τ which is small in comparison to most of the values recorded. This remains, however, a limit to the analysis and values of τ approaching 0.01 may contain gross errors.

Turbidities were not measured in cloudy conditions and would have little value. Hence, since the summer tends to have more clouds and clouds tend to occur in Broome in the mornings, there is a seasonal bias. This appears profoundly when a calibration data set of known frequency is analysed using the time sequence of the real data, giving the 10% error already mentioned. Also, a glance at the figures reveals that data are missing for nearly every year in the December-January period. This particular flaw would tend to raise the average τ since the τ values are low in this period. Some adjustment is made for this with the least squares procedure—note that the constant values in Table 3 are somewhat lower than the full averages; it is possible that the constant values from the frequency analysis are better estimates of the average τ values. The irregular nature of the data may also result in aliasing effects with anomalous harmonics appearing in the data. This should, however, be a small effect since the data were acquired at intervals of about a day and there appears to be no significant frequencies higher than one month.

It is rewarding that the sets of data at different wavelengths (Fig 6) show the same trends and that the frequency analysis produces nearly the same primary frequencies in all the data. Frequency analysis only account for about 50% of the variance observed and it appears that any reasonable harmonic analysis cannot improve on this. The remaining variance is physically acyclic, a result of instrument drift or abrupt changes, or simply random operator error. Still, the three companion measurements should, together, produce relatively valid trends and the shear number of measurements should have minimized random effects.

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